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The Life History and Post Embryonic Development of the Copepods, *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa

By Mildred H. Campbell
University of Toronto

(*Received for publication April 16, 1934*)

ABSTRACT

Calanus tonsus Brady is an abundant, deep water species in the strait of Georgia. Development is characterized by a distinct metamorphosis and the six nauplius and six copepodid stages are described.

The life cycle extends over one year and breeding occurs in the spring at the surface. The nauplii and early copepodid stages are soon replaced by stage V which dominates the plankton from May to December.

C. tonsus exists as an adult for approximately two months—January and February. Maturity is accompanied by marked degeneration of the mouth parts in both sexes, death following shortly.

The retrograde development appears associated with a change in habits. Stage V stores up reserve food, and the mature females with the disappearance of feeding devices depend upon this accumulated food during the reproductive period.

Euchaeta japonica Marukawa occurs in limited numbers in the deep water of the strait of Georgia. It undergoes a similar metamorphosis to *C. tonsus* and the twelve stages are described.

There is no definite spawning period but reproduction occurs throughout the year in deep water where development proceeds. Several broods may be produced by one female but the males are believed to die shortly after copulation.

The nauplii differ from those of *C. tonsus* due to larger size, slight increase in length from stage I to stage VI and retarded development of the appendages.

The conspicuous feature of the copepodid development is the extreme degeneration of the male mouth parts.

INTRODUCTION

During the past five years a bio-hydrographical investigation of the waters adjacent to the Fraser river mouth has been carried out under the auspices of the Biological Board of Canada. As one phase of this investigation, a preliminary quantitative study (Campbell 1929a) was made of the zooplankton occurring in the strait of Georgia during the summer and winter of 1927, and arising out of this general problem, a qualitative phase, dealing with one group of the plankton

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organisms, was investigated in some detail and about forty species of copepods were identified and described (1929 b, 1930). This study was undertaken because the copepods are present in immense numbers, dominating the plankton and forming its most stable constituent. They reproduce rapidly and may be considered as the most important of the pelagic invertebrates from an economic point of view. They furnish the primary food for the young of most marine fishes until these attain a considerable size, as well as for many of the larger planktonic animals of the various groups. The following is Willey's appreciation (1919) of the rôle of the copepods in the sea.

"The pelagic *Copepoda* are small *Crustacea* averaging less than five millimetres in length, whose abundance in the sea is the measure of their importance as a direct source of food supply for the young of the commercial fishes. In addition, they are preeminently the food of the herring which in its turn is preyed upon by larger fishes, such as the cod and halibut. Accordingly, the investigation of their distribution as governed by depth, season, currents, salinity, and temperature, is generally recognised as having an economic bearing, for fishes will necessarily assemble in places where their food is plentiful".

It seemed advisable, therefore, to continue the investigation of the group more specifically and consider in detail a few of the larger, more abundant and economically more important species of copepods. *Calanus tonsus* Brady, which constitutes the preponderant, constant element of the zooplankton in the strait of Georgia, and *Euchaeta japonica* Marukawa, a less common, larger, deep water form, were chosen as species suitable for such a detailed study. The following paper deals with the life history and larval development of these two species of copepods from British Columbia waters. The embryonic development within the egg is not discussed but the various stages in the post-embryonic development are considered in detail and compared where possible with those of other species. Various phases such as food relationships, vertical distribution, etc., are discussed in so far as they are pertinent to the general problem of life history.

The investigation was commenced during the summer of 1930 at the Pacific Biological Station, Nanaimo, B.C. The writer wishes to thank the Biological Board for the laboratory facilities provided there, especially for the use of the "A. P. Knight" which made the collection of material possible. Sincere thanks are due to Dr. W. A. Clemens, Director of the Station, whose ever helpful suggestions, kindly co-operation at all times and assistance in procuring literature are much appreciated.

The life history work has been continued during the past three years in the Department of Biology, University of Toronto. This was made possible with the assistance of National Research Council scholarships and facilities provided by Dr. B. A. Bensley. The research was directed by Dr. A. G. Huntsman, Professor of Marine Biology; his kindly suggestions, interest and valuable criticism have been very helpful. The co-operation and helpful criticism of Dr. E. M. Walker, Professor J. R. Dymond and Dr. R. E. Foerster are much appreciated. Additional data on Atlantic coast species for comparison were obtained during the summer of 1932 at the Woods Hole Oceanographic Institution,

and thanks are due to Dr. H. B. Bigelow and Dr. C. B. Wilson for their suggestions and helpful advice.

HISTORICAL REVIEW

The literature concerned with the life history and larval development of marine copepods is very scanty and though studies have been made upon a few and also upon some fresh water species as regards developmental stages, few comprehensive descriptions of sequential stages are available, such as would facilitate the recognition of the species in any particular processes of the life history.

The mature female of *Calanus tonsus* was first described by Brady (1883). The species is closely related to, yet essentially different from *C. finmarchicus* Gunnerus, the common calanoid of the Atlantic ocean. Points of difference are greater size and the absence of teeth on the basal joint of the fifth leg. The records of its distribution were chiefly from the Southern Hemisphere, southeast coast of Australia, lat. 34° 8′ S., the east coast of South America, lat. 36° 9′ S. and 36° 44′ S., and the west coast of South America, lat. 42° 43′ S. The species was also recorded between Yokohama and Sandwich islands, lat. 35° 41′ N. Thompson (1890) reported *Calanus tonsus* from the Madeira and Canary islands, lat. approximately 36°, and Bigelow (1926) observed it in the gulf of Maine. Thompson and Scott (Herdman, Thompson and Scott 1898) noted it in the mid-Atlantic—it occurred in a few gatherings from the mid-ocean where it appeared to replace *Calanus finmarchicus*. Farran (1929) recorded it chiefly at stations off New Zealand between lat. 30° to 40° S. and lat. 50° to 60° S. Records of the distribution of the species in the northern Pacific are as follows. McMurrich (1917) noted swarms of metanauplii off Esperanza inlet, Vancouver island, which might have belonged to *Calanus tonsus* rather than to *Calanus finmarchicus*. Willey (1920) recorded a few immature specimens from the Canadian Arctic Expedition station just north and west of Queen Charlotte islands, lat. 54° 30′ N., long. 159° 42′ W., indicating that *Calanus tonsus* was the species referred to without name in his report on an investigation into the Pacific halibut fisheries; at that time he saw numbers of them in an inlet to the south of Tassoo harbour on the west coast of Moresby island, south to the Christoval mountains, Queen Charlotte islands. Wailes (1929) reported *Calanus tonsus* from the strait of Georgia and the west coast of Vancouver island. Johnson (1932) has recorded its presence in Puget sound waters near the biological station at Friday harbour. All of the distributional records cited above were concerned with adult females or juveniles of the species and the mature males were not described until 1930 from the strait of Georgia (Campbell 1930).

While no work has been done previously on its life history and development, considerable information is available in the literature concerning the common Atlantic form *Calanus finmarchicus* Gunnerus. Many papers, notably those of Gran (1902), Damas (1905), Paulsen (1906), With (1915), Willey (1919),

Bigelow (1926), Russell (1925, 1927, 1928), Störmer (1929), Gibbons (1933), and Nicholls (1933), deal extensively with the biology of the latter species. As early as 1881, the nauplius stages and first copepodid stage were described by Grobben who called the species *Cetochilus septentrionalis* Goodsir. Lebour (1916) obtained almost the complete developmental series in the laboratory at Plymouth and has described them in some detail. All twelve stages have been described by Gibbons (1933).

Mature females and juvenile males of *Euchaeta japonica* Marukawa were first described in 1921 from the northern waters of Japan, lat. approximately 34° N. There are no other records of distribution of this species, but Esterly (1913) described a form as *Euchaeta elongata* from the San Diego region, California. His descriptions and plates are very incomplete, but there are apparently sufficient differences to warrant the assumption that the two species are separate.

The writer has examined samples of plankton from Monterey bay, California, through the courtesy of Dr. Tage Skogsberg of the Hopkins Marine Station, and specimens of *Euchaeta japonica* Marukawa were recognized in the samples.

Wailes (1929) recorded female specimens of *E. japonica* from the strait of Georgia and the first description of the mature males was made from specimens from that region by Campbell (1929b).

The life history and development of *Euchaeta japonica* has not been investigated previously. Until recently but brief information was available in the literature concerning the genus, but With (1915), Willey (1919), Bigelow (1926) and Störmer (1929) have given a few records of the occurrence of some of the juvenile stages of *Euchaeta norvegica* Boeck, the north Atlantic and Polar seas form. Nicholls (1934) has described the complete series of developmental stages of *E. norvegica* from the Clyde sea-area.

MATERIAL AND METHODS

The study of the life history and development of the two Pacific coast copepods, *Calanus tonsus* Brady and *Euchaeta japonica* Marukawa, was commenced during the summer of 1930. It was deemed advisable to investigate the development in the laboratory so that the various stages could be recognized as they occurred in succession in the plankton throughout the year. Attempts were made to rear the two species artificially but met with little success.

Experiments in rearing *Calanus tonsus* produced negative results. In all the plankton samples collected during the summer months of June, July and August, the copepods occurred in great numbers, but always at the same stage of development. Individuals of the fifth copepodid stage predominated and constituted the bulk of the plankton catches.

The species is obviously a very hardy one as specimens lived satisfactorily for over six weeks in unfiltered sea water at room temperature. In no case, however, was there any indication of a moult occurring during that period.

Rearing experiments for *Euchaeta japonica* produced almost negative results,

but the first two nauplius stages were obtained in this way. Larvae were hatched from the egg sacs carried by mature females and these moulted to the second nauplius stage. Freed egg clusters were kept in rearing jars and nauplii were hatched out successfully. Also nauplii of the first stage were isolated from the plankton hauls and moulted into the second nauplius stage in two days. The deep water species proved to be a less hardy one than *Calanus tonsus* and could not withstand any great range of environmental conditions in the laboratory. All specimens kept in unfiltered sea water at room temperature survived but three to four days. Better results were obtained when the individuals were kept in cooled Berkefeld filtered sea water, but the longest period of survival was eighteen days.

When experiments in rearing the animals and obtaining the larval stages in the laboratory met with such little success, it was necessary to search for the various stages in actual plankton gatherings. The *Calanus* nauplii were recognizable, due to their general similarity in size and shape to those already described and figured for *Calanus finmarchicus*. Fortunately, the earlier stages of *Euchaeta* were obtained artificially in the laboratory and as a result, the later stages could be distinguished fairly readily in the plankton.

From October 1930 to June 1931 and again in the spring of 1932, plankton samples were collected at regular intervals (twice a week when weather conditions permitted) at Station I in the middle of the strait of Georgia where the water reaches the maximum depth for the strait, 450 metres. Hauls were taken with coarse marquisette, fine voile and silk bolting cloth nets, and thus even the minute larval stages of the two species under investigation were caught. The complete series for both species were recognized, isolated and examined.

Specimens were stained in toto. Chitin staining proved rather difficult and a variety of stains were used with varying degrees of success. Iodine served very well for temporary mounts, but was found to be useless as a permanent stain. Delafield's haematoxylin, eosin, fuchsin, light green (alcoholic solution) and bleu de Lyon (alcoholic solution) were tried. Eosin proved unsatisfactory as it faded in a short time; bleu de Lyon (alcoholic solution) was not as permanent as light green (fast green) but served as an excellent stain for chitinous setae. Whole specimens as well as the dissected parts were mounted on slides in glycerine jelly.

RESULTS

Calanus tonsus Brady

It is found in abundance everywhere in the strait of Georgia. It occurs in greatest numbers in the 200 to 100 metre stratum, but is often present above and below that layer in some abundance. The average salinity at that depth is 17.17 gm. Cl. per litre and the temperature 9°C. Copepodid stages V and VI were recognized in the plankton hauls of the summer of 1930, but no additional stages were obtained by artificial rearing. From an examination of the collections taken over a year period at regular intervals (twice a week during the breeding period) all the stages of the life cycle have been obtained.

The fifth copepodid stage was found in the plankton from the middle of May until January. At this time it may be considered as the most important planktonic animal in the general economy of the strait and the same may be said for it as Damas (1905) stated for *C. finmarchicus* in the Norwegian Sea.

"En résumé *Calanus finmarchicus* est particulièrement abondant au printemps dans les régions périphériques de la Mer Norvégienne. Il y constitue un type de plankton que nous pouvons désigner comme plankton de *Calanus finmarchicus*, voulant indiquer par là, non pas que cette forme y représente toujours l'élément quantitativement prépondérant, mais bien l'élément constant".

By January 6 a few mature males were observed, and by January 29 females bearing eggs in the ovary were common. At this time the males were very numerous and outnumbered the females. The collections of March 17, 21, and 24 of 1931 were all characterized by females whose eggs were already shed. By April 13, 1931, no females with eggs were noted, but in April collection of 1930 they were fairly common.

Nauplii of stages I and II were noted by the end of January and in early February; the later stages in March. The vertical distribution of the younger nauplius stages was investigated by examination of monthly collections of plankton consisting of depth hauls from station I. In all cases, the nauplii occurred in greater numbers near the surface. By March thirty-first, the second copepodid stage was less common and the third and fourth stages occurred frequently. These were also common in the samples collected during April and May but were soon replaced by stage V.

Individuals at the different stages of development were mounted whole on slides, others dissected and mounted for detailed examination. The following descriptions are of the stages as recognized in the plankton. Each is compared, when possible, with the same stage of *Calanus finmarchicus* Gunnerus.

NAUPLIUS STAGE I (figure 1, a)

Length 0.28 to 0.30 mm. Body broadly oval, rounded at anterior end, tapering slightly towards posterior end which bears a pair of long slender feelers. Labrum conspicuous ventrally, three pairs of appendages, first antennae, second antennae and mandibles well developed.

At this stage it is slightly larger than the nauplius described by Lebour for *C. finmarchicus* and the body more tapered posteriorly.

First Antenna (figure 2, a): uniramous, elongated, apically rounded; proximal joint with short spine-like seta on distal ventral border, distal joint distinct, half as long as proximal with two long plumose setae. Appendage as a whole more slender than that described for *C. finmarchicus* but number and arrangement of setae similar.

Second Antenna (figure 2, g): coxopodite convexly rounded on inner margin; basipodite one-jointed, indistinctly divided from coxopodite, unarmed. Endopodite two-jointed, first joint large, quadrate; second joint broadly oval with two

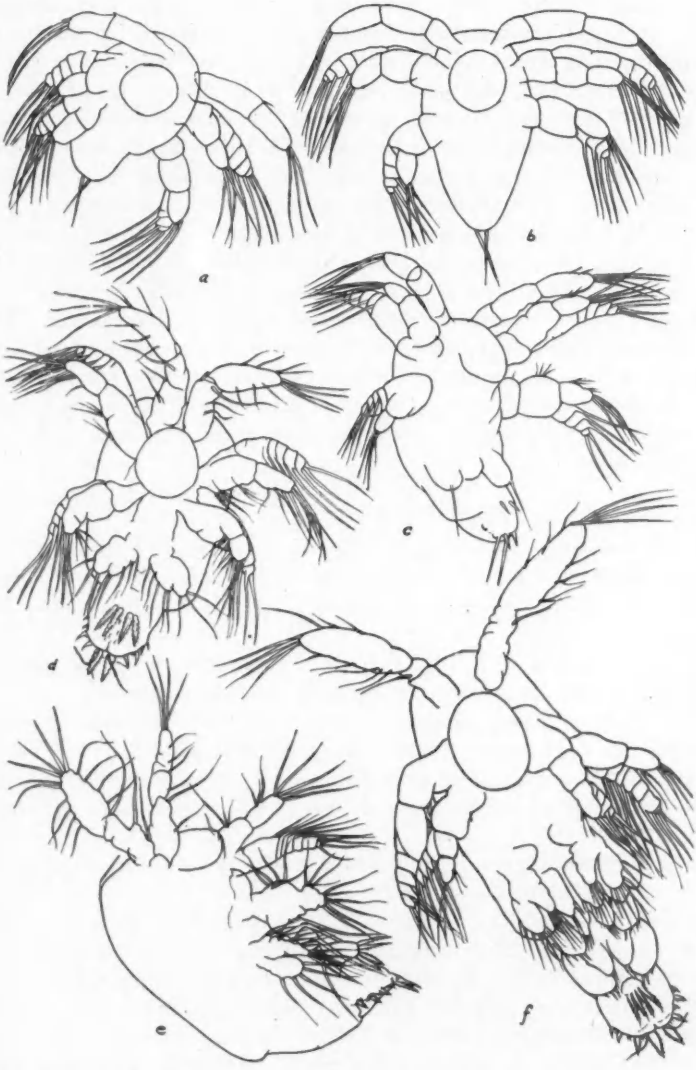

FIGURE 1. *Calanus tonsus* Brady x 44. Nauplius stages. I,—a; II,—b; III,—c; IV,—d; V,—e; VI,—f.

long terminal setae. Exopodite indistinctly divided into six segments; first segment short, broad, imperfectly divided from large quadrate second joint which bears one long plumose seta on inner margin; third to fifth joints subequal each bearing one long plumose seta on inner margin; terminal joint small with two apical setae; joints three to six together as long as terminal joint of endopodite. Appendage differs from that of *C. finmarchicus* in the absence of armature on coxopodite and basipodite. Lebour regards the basipodite as divided into two parts but from a consideration of the development this author would include distal part with endopodite. Joints of exopodite longer in *C. tonsus* than in *C. finmarchicus*, where joints three to six are shorter than terminal joint of endopodite.

Mandible (figure 3, a): coxopodite one-jointed with convex inner margin; basipodite large, quadrate, with short spine-like seta on inner convex margin; endopodite one-jointed, broadly oval with two short spine-like setae on inner margin and two long plumose terminal setae. Exopodite four-jointed, first joint quadrate, larger than others; joints one to three each with one long plumose seta on inner margin; small terminal joint with two long plumose setae. Appendage differs from that described for *C. finmarchicus* in lack of armature on basal joints; spines of endopodite shorter, joints of exopodite longer in *C. tonsus* than in *C. finmarchicus*.

NAUPLIUS STAGE II (figure 1, b)

Length 0.30 mm. Body oval in shape but more tapered posteriorly; paired appendages similar to stage I. Same stage of *C. finmarchicus* as described by Lebour smaller, more smoothly oval in shape; posterior feelers shorter than in *C. tonsus*.

First Antenna (figure 2, b): three-jointed; first joint small, unarmed; second joint three times as long as first, incompletely divided into three parts each with one plumose seta on ventral margin; of three setae, distal one largest; third joint more elongated with convex dorsal margin, same length as second and bears four terminal setae, one smaller than other three. Appendage similar to that of *C. finmarchicus* but fine spines on dorsal margin of terminal joint not present in *C. tonsus*.

Second Antenna (figure 2, h): coxopodite with two short spine-like processes on inner margin; basipodite similar to stage I; first joint of endopodite with short spine-like seta on inner margin, terminal joint more elongated with one short spine on proximal inner margin and three long terminal setae; some indication of division in second joint of exopodite, terminal joints more elongated. Appendage differs from that described for *C. finmarchicus*; number of segments in exopodite comparable according to Lebour's written description but only six joints are indicated in the accompanying figure; fifth to seventh joints together as long as terminal joint of endopodite, but in *C. finmarchicus* one-fourth that length.

Mandible (figure 3, b): coxopodite with short stubby spine on inner margin, basipodite armed with two short spine-like setae; endopodite rounded oval with

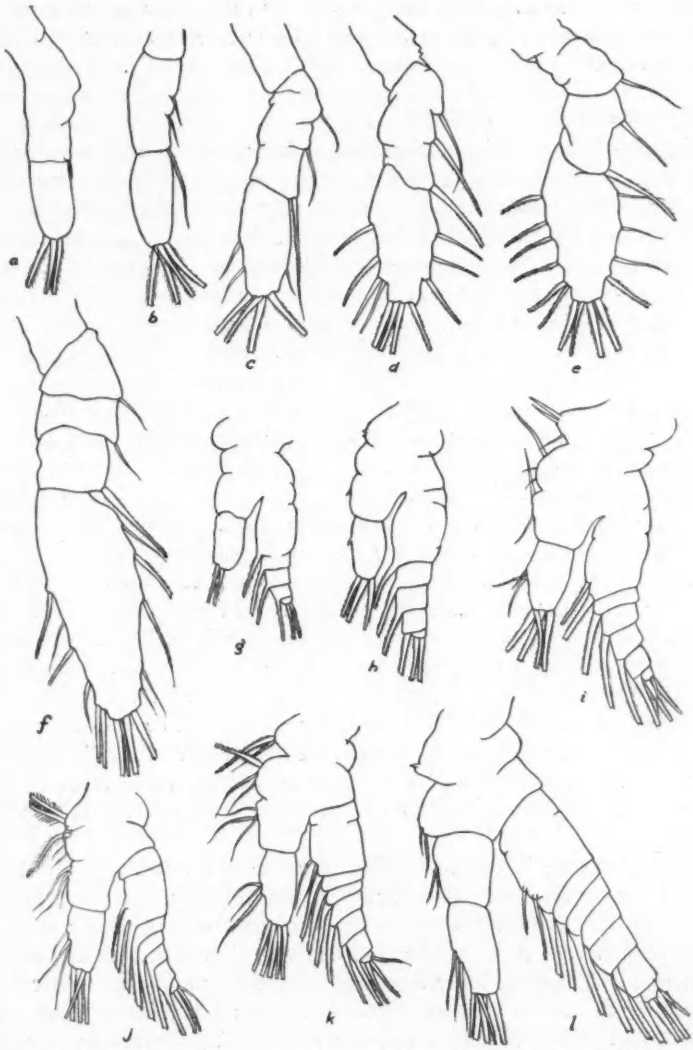

FIGURE 2. *Calanus tonsus* Brady x 122.2. Nauplius stages. I, first antenna,—a, second antenna,—g; II, first antenna,—b, second antenna,—h; III, first antenna,—c, second antenna,—i; IV, first antenna,—d, second antenna,—j; V, first antenna,—e, second antenna,—k; VI, first antenna,—f, second antenna,—l.

additional short fine, terminal seta; parts of exopodite larger. Appendage differs conspicuously from that of *C. finmarchicus* in absence of long blade on coxopodite described by Lebour as present even in stage I; short spine of endopodite represented by long setae in *C. finmarchicus* and joints of exopodite much longer than in other species.

NAUPLIUS STAGE III (figure 1, c)

Length 0.35 mm. Posterior portion of body distinct from anterior portion, armed with two long terminal feelers, pair of smooth terminal spines and pair of smaller ventral spines; curved rows of very small spines occur at bases of smooth terminal spines. Body differs from *C. finmarchicus* due to slight dorsoventral flexure; rows of small spines on abdomen less numerous in *C. tonsus*.

First Antenna (figure 2, c): second joint more conspicuously divided into three parts, each lobe with one seta, most distal seta coarser than others, extending beyond end of terminal joint; third joint with one short fine seta on distal ventral border and two slightly longer fine setae on dorsal margin in addition to four terminal setae described for stage II. Appendage more elongated than that described for *C. finmarchicus*; second joint approximately two and a half times as long as broad but only twice as long in *C. finmarchicus*; terminal joint more rectangular in shape in *C. tonsus*.

Second Antenna (figure 2, i): coxopodite armed with two smooth blade-like spines and one slender seta on inner margin, basipodite with one long smooth blade and two fine setae; first joint of endopodite with two slender setae on inner margin, second joint with three fine setae on inner margin and four terminal setae; exopodite more definitely seven-jointed, first joint imperfectly separated from second which bears one fine and one coarse plumose setae. Of joints three to six, third shorter and broader than others, each with one coarse seta on inner margin; terminal joint with two long plumose setae and additional fine seta. Armature of coxopodite not as extensive as that figured for *C. finmarchicus*; number of setae on exopodite same for both species but joints three to seven in *C. tonsus* twice as long as joint two, while in *C. finmarchicus* half as long as joint two.

Mandible (figure 3, c): coxopodite with one fine seta and basipodite with four equal slender setae on convex inner margin of joint; endopodite broader at proximal end with slight indication of division into two parts; inner elevation of proximal portion with three slender and one very fine setae, distal portion with two slender equal setae on inner border and three long and one shorter terminal setae—row of fine spines at bases of terminal setae; first joint of exopodite with two large setae. Basipodite more quadrate than in *C. finmarchicus,* lacking long masticatory bristle but with additional fine setae; endopodite more elongated and four proximal setae grouped together, not in twos, as in *C. finmarchicus,* terminal setae larger than others but in *C. finmarchicus* all setae of endopodite approximately the same size, two setae of first joint of exopodite almost subequal, but in *C. finmarchicus* proximal seta finer and shorter than distal seta.

NAUPLIUS STAGE IV (figure 1, d)

Length 0 46 mm. Body flexed dorso-ventrally, abdomen distinct from broader anterior portion; armature of posterior end consists of two pairs of ventral spines, one pair larger, denticulate terminal spines and four pairs lateral spines—lateral spines smaller than either terminal or ventral spines, and of four pairs, two more distal larger than two proximal pairs; curved rows of small spines at bases of lateral spines. First maxillae evident as small bilobed structures.

First Antenna (figure 2, d): joints one and two similar to stage III but setae of second joint coarser; terminal joint broader with three setae on ventral border, four on dorsal border and four terminal setae; of dorsal setae, two most distal arise together, one very slender. Appendage similar to that described by Lebour for *C. finmarchicus* but dorsal setae are not equidistant apart and fine hooks on dorsal border are lacking.

Second Antenna (figure 2, j): coxopodite armed with two coarsely setose masticatory bristles and one short fine seta, basipodite with one coarsely setose bristle; first joint of endopodite with two long and one shorter setae, second joint similar to stage III, but two longer setae of lateral group increased in length; exopodite seven-jointed, second joint with one fine and two coarse setae, joints three to seven similar to stage III. In *C. tonsus* the endopodite extends as far as the distal end of the fifth joint of exopodite, but in *C. finmarchicus* endopodite only reaches end of second joint; joints three to six approximate length of one and two, but in *C. finmarchicus* they are considerably shorter than first two.

Mandible (figure 3, d): coxopodite broader and shorter with definite masticatory edge on inner margin; basipodite now bears five plumose setae on inner margin and a rounded projection on distal border between endopodite and exopodite; endopodite with rounded elevation on inner margin and seven setae; of these, five proximal setae grouped, two more slender than others; remaining two distal; narrower terminal portion of endopodite with four equal setae. Joints of exopodite shorter and broader. Coxopodite larger than in *C. finmarchicus*, basipodite quadrate with an additional seta; lobe between endopodite and exopodite absent and first seta of exopodite finer in *C. finmarchicus*.

First Maxilla (figure 3, g): appendage sometimes called maxillula; coxopodite and basipodite undifferentiated, endopodite narrower than exopodite with three lobes indicated on outer margin; each with one plumose seta and there are two terminal setae. Exopodite imperfectly separated from endopodite with three equal plumose setae. In *C. finmarchicus* there are only four setae on endopodite.

NAUPLIUS STAGE V (figure 1, e)

Length 0.56 mm. Dorso-ventral flexure more pronounced, armature of posterior end similar, an indication of segmentation in abdomen. First maxillae with parts of fully developed appendage now recognizable.

First Antenna (figure 2, e): five joints indicated; ventral border of terminal joint with four setae, three proximal, fine and slender; dorsal border with six

setae, four terminal setae. Lebour's plate for this appendage similar but only three ventral setae described.

Second Antenna (figure 2, k): armature of coxopodite slightly reduced, one masticatory bristle smaller, fine seta absent; basipodite and endopodite similar to stage IV; exopodite appears eight-jointed, first joint short and broad, second joint square with two fine and one coarse setae, three and four similar to joint one, five to seven successively longer, each with one coarse seta, terminal joint very small with three setae. In *C. finmarchicus,* four setae on inner margin of terminal joint of endopodite.

Mandible (figure 3, e): appendage similar to stage V; five proximal setae on lateral elevation of endopodite definitely grouped together, other two situated near four terminal setae. In *C. finmarchicus,* number of setae same on endopodite but arranged differently; second seta on first joint of exopodite considerably coarser than first but in *C. tonsus* equal.

First Maxilla (figure 3, h): coxopodite partially divided into three external lobes and one internal lobe, first external lobe or gnathobase indicated as rounded elevation, other two external lobes each with two long slender setae, internal lobe or epipodite a rounded elevation, unarmed; basipodite imperfectly divided from coxopodite with two slender setae on inner margin; endopodite one-jointed, broad at base tapering toward distal end with two slender setae on inner margin and four terminal setae; exopodite a large rounded oval joint with five setae. Appendage as described by Lebour for *C. finmarchicus* not so well developed; coxopodite similar to *C. tonsus* in armature but endopodite more rounded with fewer setae, not clearly differentiated from basipodite.

NAUPLIUS STAGE VI (figure 1, f)

Length 0.70 mm. Body elongated, indication of two segments in abdomen, posterior end with additional armature of fine spines at bases of lateral hooks; maxillipeds evident as elongated lobes in middle line; first and second pairs swimming legs indicated as primitive bilobed structures toward posterior end. This stage of *C. finmarchicus* not described by Lebour, was observed by Grobben (1881) for the same species, then called *Cetochilus septentrionalis,* and this author has examined specimens from strait of Georgia; Gibbons (1933) has described this stage. *C. tonsus* is more elongated than *C. finmarchicus* and body straighter; terminal spines larger than lateral ones in *C. tonsus* but those figured by Grobben for *Cetochilus septentrionalis* smaller; ventral hooks in *C. tonsus* longer than those figured by either Grobben or Oberg; abdomen with square end in *C. tonsus* but distinctly tapered in *C. septentrionalis.* Length of Grobben's stage of *C. septentrionalis* 0.64 mm; specimens of *C. finmarchicus* observed from strait of Georgia, 0.8 mm. Gibbons (1933) recorded specimens of *C. finmarchicus,* 0.81 mm.

First Antenna (figure 2, f): five-jointed, first joint unchanged, second to fourth joints broader than long, each with one seta; setae of second and third joints finer than in earlier stages but that of fourth joint still long and coarse. Fifth joint three times as long as broad tapering toward distal end with five setae

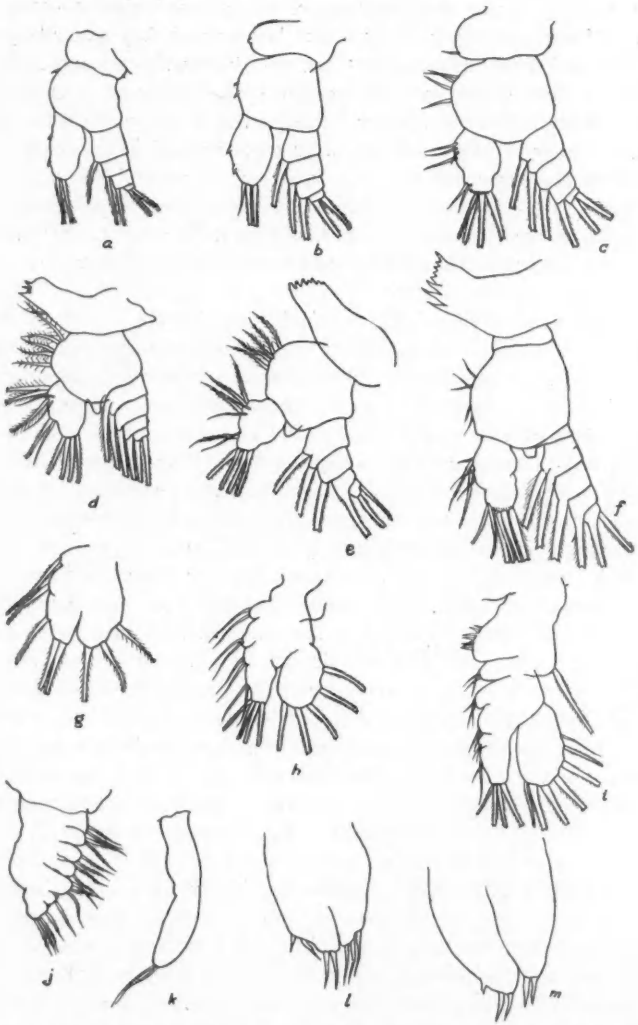

FIGURE 3. *Calanus tonsus* Brady x 122.2. Nauplius stages. I, mandible,—a; II, mandible,—b; III, mandible,—c; IV, mandible,—d, first maxilla,—g; V, mandible,—e, first maxilla,—h; VI, mandible,—f; first maxilla,—i, second maxilla,—j, maxilliped,—k, first leg,—l, second leg,—m.

on ventral border; first or most proximal seta short and fine resembling fourth, second and third slightly longer and coarser, fifth or most distal seta shortest, finer than in stage V; of six dorsal setae, first situated approximately one third along joint, third, two thirds along dorsal border and they are subequal, second between first and third, shorter and finer, fourth seta shorter and fifth and sixth arise together near distal end. No detailed description of this appendage of *C. septentrionalis* by Grobben, but in figure of the complete larva the second joint is still incompletely divided with but two setae; terminal joint with same number of setae as in *C. tonsus* but only two indicated on ventral border and eight on dorsal border. In specimens of *C. finmarchicus* examined by this author from the strait of Georgia, the terminal joint of first antenna is shorter, only twice as long as wide, dorsal margin definitely concave; fifteen setae, five ventral, six dorsal and four terminal as in *C. tonsus*.

Second Antenna (figure 2, 1): coxopodite considerably modified, masticatory bristle of stage V absent, only one short spine persisting; convex inner margin of basipodite with two short fine setae but coarsely setose bristle lacking; joints of endopodite similar in shape to stage V but terminal joint more elongated, first joint with only two fine setae. Basal joints are clearly shown by Grobben for *C. septentrionalis*; *C. tonsus* differs conspicuously in the reduction of the armature on coxopodite and basipodite. In *C. tonsus* there are three setae on inner margin of terminal joint of endopodite, but Grobben indicates but two setae. Number of joints and setae of exopodite is not clearly shown by Grobben.

Mandible (figure 3, f): teeth on masticatory edge of coxopodite more numerous and setae on basipodite much reduced; endopodite more definitely divided into two parts, first joint with two long and three shorter setae which are smaller than in stage V, second joint with two slender setae near distal end and four long terminal setae; first joint of exopodite partially divided into two, joints two to four more elongated and quadrate. Setae of basipodite much reduced in *C. tonsus* compared with those figured by Grobben for *C. septentrionalis* and by Gibbons for *C. finmarchicus*. Grobben indicates only seven setae on endopodite but Gibbons shows ten. Exopodite of *C. septentrionalis* with only five setae according to Grobben but Gibbons figures six for *C. finmarchicus* as in *C. tonsus* but proximal seta fine.

First Maxilla (figure 3, i): gnathobase larger than other internal lobes, rounded, with seven very short spine-like setae; each of smaller internal lobes oval-shaped with three fine setae; epipodite with one long coarse plumose seta; basipodite larger with two fine setae on distal inner margin of joint; endopodite partially divided into two joints, first small, with two fine setae, second large, broad at base, tapering toward distal end with two slender setae on proximal inner margin and four large terminal setae of which innermost is finest; exopodite large, oval, with seven setae, innermost of terminal group and two proximal setae of outer margin more slender than other four. Appendage more elongated than that described by either Grobben or Gibbons; large internal lobe of coxopodite not described for *C. septentrionalis* but shown by Gibbons; two smaller

internal lobes figured by Grobben with one and two setae respectively, and by Gibbons each with four setae. Epipodite not shown by Grobben but figured by Gibbons. Only four setae are figured for basipodite and endopodite by Grobben but Gibbons pictures nine as compared with ten in *C. tonsus*; only five setae are figured by Grobben on exopodite but seven by Gibbons as in *C. tonsus*; exopodite more rounded in *C. finmarchicus* and *C. septentrionalis* than in *C. tonsus*.

Second Maxilla (figure 3, j): appendage sometimes called first maxilliped; uniramous, incompletely divided into lobes; first four considered as belonging to coxopodite, each with two fine setae; fifth lobe or basipodite larger than others with three fine setae; terminal portion or endopodite narrower than basal portion, slightly divided into three lobes, each of proximal lobes with one seta and terminal lobe with three setae. Appendage imperfectly indicated by Grobben as lobe with four setae.

Maxilliped (figure 3, k): one-jointed, elongated, with two terminal setae. Grobben indicates three terminal and one lateral setae for *C. septentrionalis*.

First Leg (figure 3, l): inner lobe partially separated from basal part with three terminal setae; outer lobe broader than inner with two terminal setae and two shorter spine-like setae on proximal outer margin. Grobben indicates about seven setae on inner lobe and five on outer; Oberg figures three on inner and two on outer lobe. Outer lobe or exopodite on left of illustration—all swimming legs of later stages drawn in same way.

Second Leg (figure 3, m): similar to first leg; inner lobe with two terminal setae, outer lobe with two terminal setae and one seta on distal outer margin. Grobben's figure for *C. septentrionalis* shows three setae on inner and none on outer lobe.

COPEPODID STAGE I (figure 4, a)

Length 0.9 to 1.0 mm. Body straight, resembles adult in general shape; anterior portion with three free thoracic segments sharply cut off from posterior portion with caudal furca; furca with three long and one short terminal setae and one short inner seta. First antennae elongated, held at right angles to body serving as balancing structures; two pairs of swimming legs well developed, additional third pair evident. *C. finmarchicus* observed by this author from gulf of Maine as very similar to *C. tonsus*, but *C. septentrionalis* described by Grobben as slightly larger with five caudal setae.

First Antenna (figure 4, a): appendage now an elongated, eleven-jointed, cylindrical balancing structure, due to multiple division in terminal joint; antepenultimate and penultimate segments with long sensory bristles. Appendage as described by Lebour for *C. finmarchicus* very similar, but Grobben indicates but eight segments for *C. septentrionalis*.

Second Antenna (figure 4, d): coxopodite with one long plumose seta on inner distal margin; basipodite quadrate with two setae, one plumose and one simple, on inner distal margin. Endopodite composed of two sub-equal joints; first longer than in nauplius VI with two slender simple setae situated nearer

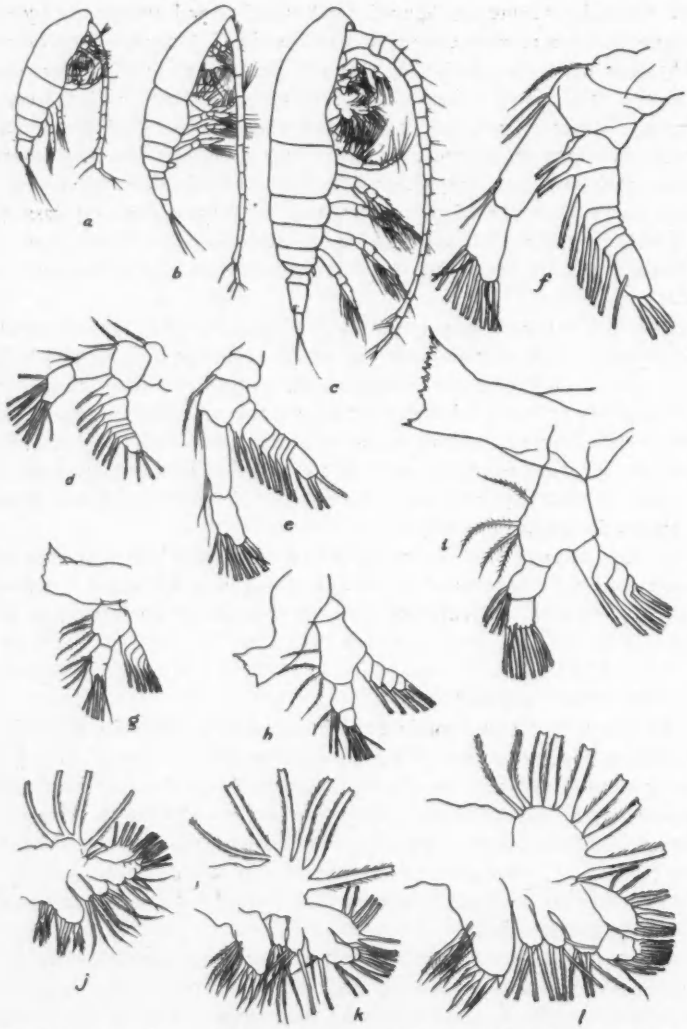

FIGURE 4. *Calanus tonsus* Brady. Copepodid stages. I, whole animal x 11.66,—a, second antenna x 44,—d, mandible x 44,—g, first maxilla x 44,—j; II, whole animal x 11.66, —b, second antenna x 44,—e, mandible x 44,—h, first maxilla x 44,—k; III, whole animal x 11.66,—c, second antenna x 44,—f, mandible x 44,—i, first maxilla x 44,—l.

distal border of inner margin, second joint with group of four long equal setae on inner elevation and six terminal setae, one more slender than others. Exopodite seven-jointed; joints one and two subequal, each with two heavy smooth setae on inner margin; joints three to six subequal, each with one seta similar to those of joints one and two; joint seven as long as two but narrower with one fine plumose lateral seta and three smooth terminal setae. Considerable modification of the exopodite noticeable; number of setae same as in nauplius VI with a rearrangement; some of joints demonstrate tendency to telescope into each other. Appendage similar to that described by Lebour for *C. finmarchicus* but bears additional terminal seta on endopodite; six terminal setae described by Grobben but only three figured on inner elevation. Arrangement of setae differs in two species—in *C. finmarchicus* joint one bears only one seta, and joint two, three setae. Terminal joint of exopodite shorter and broader in *C. tonsus* than in that described by Lebour; exopodite not clearly indicated by Grobben.

Mandible (figure 4, g): teeth on masticatory edge of coxopodite shorter, more numerous; setae of basipodite larger; definite indication of two joints in endopodite, setae on inner elevation of first joint reduced to four, second joint with six terminal setae, two more slender than others. Exopodite five-jointed, joints shorter and broader than in nauplius VI; joints one to four each with one coarse plumose seta on inner margin, joint five with two terminal plumose setae. Appendage resembles *C. finmarchicus* according to Lebour; Grobben shows only four terminal setae on endopodite, exopodite not clearly indicated, toothed process larger and more angular in *C. tonsus*.

First Maxilla (figure 4, j): appendage considerably modified; basal portion larger in comparison to terminal portion, whole maxilla shorter and more foliaceous in appearance. Gnathobase armed with ten spike-like bristles; each of smaller lobes oval in shape, most internal one armed with four, external one armed with three plumose setae; epipodite with four coarse plumose setae; an additional very small external lobe with one fine plumose seta; basipodite with two long and one short plumose setae; endopodite incompletely divided into three joints, first with three, second with three, terminal joint with four plumose setae; exopodite reduced with seven plumose setae. First maxilla of *C. finmarchicus* figured by Lebour with six, and by Grobben with eight bristles on gnathobase, which is smaller. Lebour and Grobben both show two setae on each of smaller internal lobes of coxopodite, but Lebour figures three, Grobben four coarse setae on large external lobe of coxopodite.

Second Maxilla (figure 5, a): flattened uniramous appendage; coxopodite composed of four lobes, first with three equal coarse setae, second to fourth with two coarse and one smaller setae; basipodite one-lobed with three coarse setae as in nauplius VI; endopodite three-jointed, joints one and two each with one coarse plumose seta and one slender finer seta, joint three with two coarse plumose setae and one fine bristle. Appendage differs in *C. finmarchicus* in the presence of an additional seta on the first lobe of coxopodite, according to Lebour; Grobben's figure shows one less seta on lobes one, three and four of coxopodite; an undivided

endopodite indicated by Grobben with only four setae as compared with seven in *C. tonsus.*

Maxilliped (figure 5, d) : uniramous, longer than second maxilla; coxopodite with two slender distal setae and two small prominences, first armed with one coarse plumose seta, second with one coarse and one very fine plumose seta; basipodite with two plumose setae toward distal end of joint; endopodite two-jointed, first joint elongated with two fine setae proximally and one plumose seta distally, second joint very short with four terminal setae, one more slender than others. In *C. finmarchicus* setae of coxopodite finer, three setae on basipodite as described by Lebour; two setae indicated on coxopodite by Grobben; no segmentation in endopodite.

First Leg (figure 5, g) : coxopodite and basipodite each one-jointed, unarmed; endopodite unsegmented with seven plumose setae, four on inner margin, two terminal, one on outer margin; exopodite one-jointed with two plumose setae on inner border, one terminal seta, a terminal blade and short spine, two short spines on outer margin. Only four setae indicated by Lebour and Grobben on endopodite of *C. finmarchicus*; three short spines on outer margin of exopodite and one short terminal spine shown by Grobben.

Second Leg (figure 6, a) : coxopodite and basipodite each one-jointed, basipodite with small spine on outer border; endopodite undivided with six plumose setae, three on inner margin, two terminal, one on outer margin; exopodite one-jointed with two plumose setae on inner margin, one terminal plumose seta, one toothed terminal blade, two small terminal spines and two small spines on outer margin. In *C. finmarchicus,* spine on basipodite not indicated by Lebour; only five setae shown on endopodite but Grobben figures six as in *C. tonsus.*

COPEPODID STAGE II (figure 4, b)

Length 1.3 to 1.4 mm. Body divided into four thoracic segments and two abdominal segments; three pairs swimming legs developed, a rudimentary fourth pair indicated. *C. finmarchicus* slightly smaller at this stage, 1.2 mm. in length, but number of setae on caudal furca greater than in *C. tonsus.*

First Antenna (figure 4, b) : antenna eleven-jointed.

Second Antenna (figure 4, e) : appendage larger, some joints more elongated; first joint of endopodite almost twice length of second joint which bears an additional seta on inner margin; terminal joint of exopodite twice as long as broad.

Mandible (figure 4, h) : teeth on masticatory edge of coxopodite more numerous, anterior margin with concave border, endopodite two-jointed with seven terminal setae; joints of exopodite more elongated. Lebour indicates only six terminal setae on endopodite for *C. finmarchicus.*

First Maxilla (figure 4, k) : gnathobase with similar armature to stage I; each of two smaller lobes with four plumose setae; epipodite with six large setae, one smaller than others; terminal joint of endopodite with five setae. In *C. finmarchicus,* seven large setae on external lobe of coxopodite.

Second Maxilla (figure 5, b) : first lobe of coxopodite with four setae, lobes

FIGURE 5. *Calanus tonsus* Brady. Copepodid stages x 44. I, second maxilla,—a, maxilliped, —d, first leg,—g; II, second maxilla,—b, maxilliped,—e, first leg,—h; III, second maxilla,—c, maxilliped,—f, first leg,—i.

two to four similar to stage I; basipodite with four setae; first joint of endopodite with two coarse and one fine setae, second and third joints similar to stage I. In *C. finmarchicus,* basipodite with only three setae.

Maxilliped (figure 5, e): coxopodite larger with three prominences; proximal elevation bears one coarse plumose seta; second, one coarse and one very slender fine seta; third, two coarse and one very fine seta; distal portion bears three slender plumose setae; basipodite with row of very short spines along proximal border of joint; endopodite three-jointed, joint one with three plumose setae, joint two with one plumose seta, terminal joint similar to stage I. In *C. finmarchicus* coxopodite figured with only two coarse setae as in stage I.

First Leg (figure 5, h): coxopodite with a plumose seta on inner margin; basipodite armed with curved plumose seta arising on inner distal margin; endopodite two-jointed, first joint with one plumose seta on inner margin, second joint with seven setae, four on inner margin, two terminal, one on outer border; exopodite two-jointed, first joint with slender curved spine on distal outer margin, second joint with one smaller and two large setae on inner setose margin, a terminal seta, a terminal blade and a slender curved spine and two slender spines on outer margin. Appendage differs from that of *C. finmarchicus* in general shape; in *C. tonsus* first joints of both exopodite and endopodite are larger, second joint of exopodite slightly concave on outer proximal border; in *C. finmarchicus* no setae are figured on either coxopodite, basipodite or first joint of endopodite.

Second Leg (figure 6, b): coxopodite now bears a plumose seta on inner margin; endopodite two-jointed, first joint with one plumose seta on inner margin, second joint with seven setae, three on inner margin, two terminal, two on outer margin; exopodite two-jointed, first joint with two small spines on distal outer margin, finely setose on inner margin; second joint with three setae on inner margin, one terminal seta, one terminal blade, two small terminal spines and one small spine on outer margin. In *C. finmarchicus,* seta on coxopodite and spine on basipodite not indicated by Lebour; only one spine shown on distal outer border of first joint of exopodite.

Third Leg (figure 6, d): coxopodite one-jointed, smooth; basipodite bears small spine on outer margin; endopodite unsegmented with six setae, three on inner margin, two terminal, one on outer margin; exopodite one-jointed with three setae on inner margin, one terminal blade, two short terminal spines and two short spines on outer margin. In *C. finmarchicus,* no spine on basipodite, only one short terminal spine on exopodite.

COPEPODID STAGE III (figure 4, c)

Length 1.8 mm.; five free thoracic segments, two abdominal segments; four pairs swimming legs well developed, rudiments of a fifth pair indicated. In *C. finmarchicus,* according to Lebour, there is no increase in size over previous stage; With (1915) reported specimens of *C. finmarchicus* averaging 1.4 to 1.7 mm. in length; the author has observed individuals from the gulf of Maine averaging 1.4 to 1.8 mm.

First Antenna (figure 4, c): twenty-jointed. In *C. finmarchicus* only sixteen segments figured by Lebour at this stage, but this author has examined specimens of the species from gulf of Maine with antennae twenty-two jointed.

Second Antenna (figure 4, f): appendage larger, terminal joint of endopodite with six setae on inner margin. In *C. finmarchicus,* the author has observed additional fine setae on outer distal margin of terminal joint of endopodite in specimens from gulf of Maine.

Mandible (figure 4, i): teeth on masticatory edge of coxopodite more numerous, each tooth with several prongs; a small plumose seta at one edge of cutting surface; terminal joint of endopodite with eight setae.

First Maxilla (figure 4, l): large external lobe of coxopodite with eight large setae, two less coarse than others; basipodite with four setae; three setae on first joint of endopodite; exopodite with eight setae. In *C. finmarchicus,* according to Lebour, gnathobase armed with only eight spike-like bristles, two smaller internal lobes of coxopodite each with three setae, exopodite and epipodite each with one more seta. Specimens examined from gulf of Maine show maxilla very similar to *C. tonsus.*

Second Maxilla (figure 5, c): first lobe of coxopodite with five large setae, other lobes similar to stage II. In *C. finmarchicus,* appendage is said to resemble adult and first lobe of coxopodite should therefore bear six setae.

Maxilliped (figure 5, f): coxopodite with additional fine seta at base of fourth coarse seta, distal elevation with four slender setae and several very fine hair-like setae; basipodite armed with five setae, three more proximally situated than others; endopodite four-jointed, first joint with three setae, second with one plumose seta, third joint with two setae, one on inner and one on outer margin, fourth joint with four setae, three more terminally placed than fourth.

First Leg (figure 5, i): joints of exopodite and endopodite more elongated, second joint of endopodite now bears eight setae, five on inner margin, two terminal and one on outer margin; first joint of exopodite finely setose with one plumose seta on inner margin in addition to a slender spine on outer margin; second joint finely setose along proximal inner margin with an additional seta on inner margin and terminal spine now longer than either of two outside spines, all more slender than in stage II. In Lebour's figures for *C. finmarchicus,* coxopodite and basipodite as yet unarmed, second joint of endopodite with only seven setae, first joint of exopodite with no outside spine, second joint with four spines instead of three as in *C. tonsus.* In gulf of Maine specimens examined, appendages agreed well with *C. tonsus.*

Second Leg (figure 6, c): coxopodite and basipodite similar to stage II; endopodite two-jointed, second joint now bearing eight plumose setae, four on setose inner margin, two terminal and two on outer margin; second joint of exopodite now bears four setae on inner setose margin, a terminal seta and blade, two short terminal spines and two short spines on outer margin. In *C. finmarchicus,* nine setae are indicated by Lebour on terminal joint of endopodite and only one

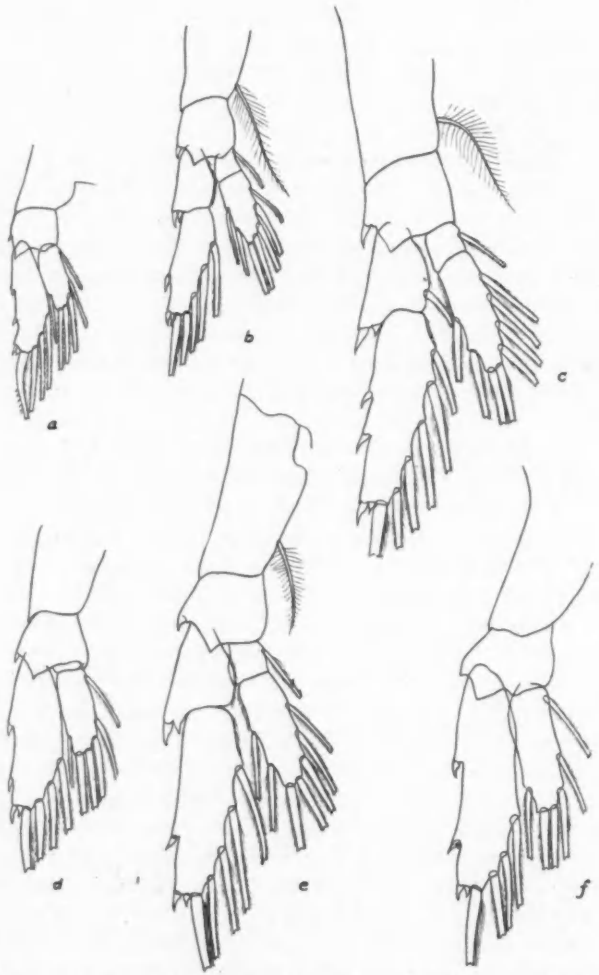

FIGURE 6. *Calanus tonsus* Brady. Copepodid stages x 44. I, second leg,—a; II, second leg,—b, third leg,—d; III, second leg,—c, third leg,—e, fourth leg,—f.

distal outer spine on first joint of exopodite; specimens of *C. finmarchicus* examined did not exhibit differences but were similar to *C. tonsus*.

Third Leg (figure 6, e): coxopodite now bears a plumose seta on inner margin; basipodite as in stage II; endopodite two-jointed, the first with one plumose seta on inner margin, second with seven setae, three on inner margin, two terminal and two on outer setose margin; exopodite two-jointed, first joint with two short spines on distal outer margin, finely setose along inner margin; second joint finely setose with four setae on inner margin, a terminal blade, two short terminal spines and one short spine on outer margin. In *C. finmarchicus* no inside seta indicated by Lebour on coxopodite; first joint of exopodite with one seta on inner margin in addition to spines on outer margin.

In gulf of Maine specimens of *C. finmarchicus* inside seta of coxopodite evident; no seta on inner margin of first joint of exopodite but cluster of long fine hairs present.

Fourth Leg (figure 6, f): coxopodite and basipodite each one-jointed, unarmed; endopodite unsegmented with six setae, three on inner margin, two terminal and one on outer margin; exopodite one-jointed with three setae on inner margin, a terminal blade, two short terminal spines and two short spines on outer margin. In specimens of *C. finmarchicus* examined, the inner margin of exopodite was finely setose.

COPEPODID STAGE IV (figure 7, a)

Length 2.8 to 3.0 mm. Three abdominal segments indicated; five pairs swimming legs well developed. No definite length recorded for this stage of *C. finmarchicus* by Lebour; reported by With (1915) as 2.8 to 2.9 mm. in length; gulf of Maine specimens averaged 2.3 to 2.6 mm.

First Antenna (figure 7, a): twenty-four jointed.

Second Antenna (figure 7, e): terminal joint of endopodite with six setae on inner margin as in stage III, seven terminal setae; outer margin of second joint now finely setose. In *C. finmarchicus* seven setae figured by Lebour on inner margin of second joint of endopodite.

Mandible (figure 7, i): coxopodite with nine terminal setae, two finer than others. In *C. finmarchicus* only eight terminal setae according to Lebour, nine observed by author as in *C. tonsus*.

First Maxilla (figure 8, a): gnathobase armed with thirteen spike-like bristles; epipodite now bears nine large setae, two less coarse than others; endopodite similar to stage III but exopodite now bears nine setae.

Second Maxilla (figure 8, d): first lobe of coxopodite now with six setae; remaining lobes with exception of terminal one same as in stage III—terminal lobe with additional seta; appendage now same as in adult stage.

Maxilliped (figure 8, h): coxopodite and basipodite similar to stage III; endopodite five-jointed, first joint with four setae, second with two, joint three with one seta, joint four with one seta on inner and one on outer margin, joint five with four terminal setae. In *C. finmarchicus*, endopodite described by Lebour

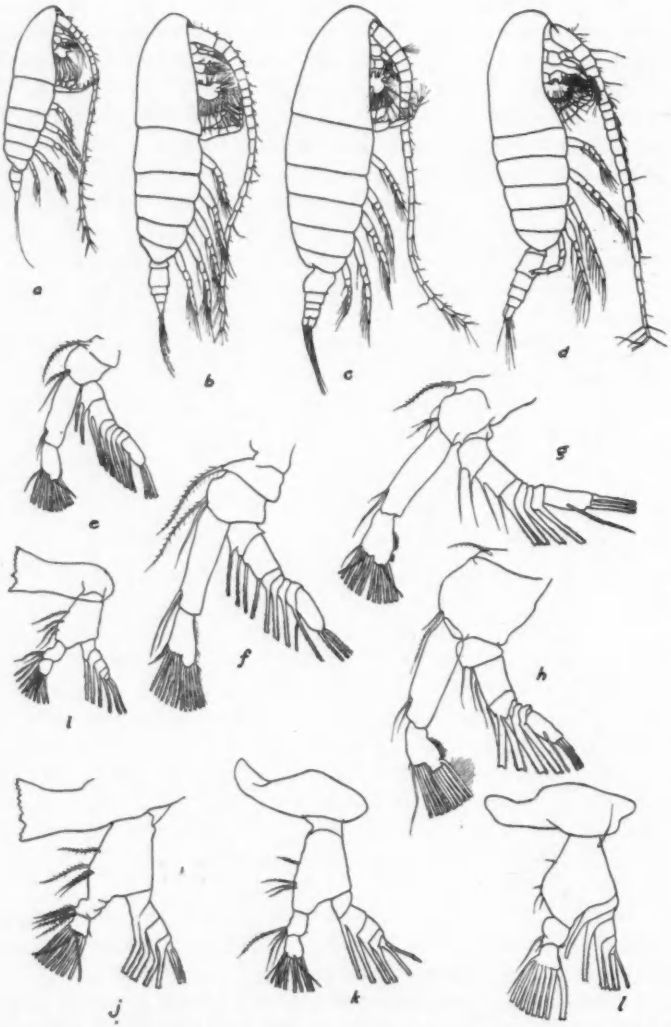

FIGURE 7. *Calanus tonsus* Brady. Copepodid stages. IV, whole animal x 4.33,—a, second antenna x 27.8,—e, mandible x 27.8,—i; V, whole animal x 4.33,—b, second antenna x 27.8,—f, mandible x 27.8,—j; VI ♀ whole animal x 4.33,—c, second antenna x 27.8, —g, mandible x 27.8,—k; VI ♂ whole animal x 4.33,—d, second antenna x 27.8,—h, mandible x 27.8,—l.

as only four-jointed, joint three bearing two setae on inner margin and one on outer margin; in gulf of Maine specimens of *C. finmarchicus* examined by author endopodite definitely five-jointed, segment corresponding to joint three with only one seta on inner margin.

First Leg (figure 8, l): appendage similar to stage III, joints slightly more elongated. In Lebour's description of *C. finmarchicus* no seta indicated on inner margin of basipodite, terminal joint of endopodite bears but six setae, although described with seven setae in stage III; differences not apparent in specimens examined from gulf of Maine.

Second Leg (figure 9, a): coxopodite bears cluster of fine setae proximal to plumose seta on inner margin; endopodite two-jointed, first joint as in stage III but outer margin finely setose, second joint with nine setae, five on inner margin, two terminal and two on outer margin; exopodite similar to stage III, but outer margin of second joint finely setose. In gulf of Maine specimens examined second outer spine of exopodite situated equidistant between first outer spine and terminal spine.

Third Leg (figure 9, d): coxopodite now bears fine hairs in addition to seta on inner margin; endopodite two-jointed, joint one as in stage III but finely setose on outer margin, second joint with eight setae, four on inner margin, two terminal and two on outer setose margin; first joint of exopodite now bears a seta on inner margin in addition to spines on outer margin, second joint with five setae on inner margin, a terminal blade, two short terminal spines and two short spines on outer setose margin. In *C. finmarchicus* only one spine indicated by Lebour on outer margin of first joint of exopodite and four setae on inner margin of second joint. Gulf of Maine specimens found to be very similar to *C. tonsus* except in arrangement of spines on terminal joint of exopodite; second outer spine situated nearer terminal spine, not equidistant between it and first spine.

Fourth Leg (figure 9, e): coxopodite with a plumose seta on inner margin; endopodite two-jointed, first joint with one seta on inner margin and a short blunt spine on outer margin, second joint with seven setae, three on inner margin, two terminal and two on outer setose margin; exopodite two-jointed, first joint finely setose on inner proximal margin with two short spines on outer distal border, second joint finely setose on inner proximal border with five setae on inner margin, a terminal blade, two short terminal spines and two short spines on outer margin. In *C. finmarchicus* only four setae shown by Lebour on inner margin of second joint of exopodite but five observed in gulf of Maine specimens.

Fifth Leg (figure 9, h): coxopodite and basipodite each one-jointed, basipodite with short spine on outer margin; endopodite unsegmented with five setae, two on inner margin, two terminal and one on outer margin; exopodite one-jointed with three setae on inner margin, a terminal blade, two short terminal spines and two short spines on outer margin. According to Lebour, no spine present on outer margin of coxopodite; only one short terminal spine indicated on exopodite in *C. finmarchicus*. The gulf of Maine specimens examined exhibited

spine on coxopodite but six setae on endopodite compared with only five in *C. tonsus.*

COPEPODID STAGE V (figure 7, b)

Length 4.5 to 5.0 mm.; five thoracic segments as in stage IV; abdomen four-jointed, second segment at least twice as long as any one of other abdominal segments; five pairs swimming legs well developed. Lebour gives no definite record of length of *C. finmarchicus* but With (1915) observed it to average 2.2 to 2.5 mm.; gulf of Maine specimens average 3.3 to 3.7 mm.; fourth abdominal segment figured by Lebour as longer than others; With (1915) records second segment longest as in *C. tonsus.*

First Antenna (figure 7, b): twenty-four jointed.

Second Antenna (figure 7, f): second joint of endopodite with eight setae on inner margin and seven terminal setae; appendage completely developed resembling adult stage.

Mandible (figure 7, j): mandible now as in adult stage with ten terminal setae on endopodite; additional very small seta on outer margin of terminal joint.

First Maxilla (figure 8, b): gnathobase of coxopodite with fourteen spine-like bristles, five more slender than others, lobe finely setose near base; other lobes of coxopodite as in stage IV; endopodite as in stage IV; exopodite with ten setae.

Second Maxilla (figure 8, e): appendage similar to stage IV, resembling that of *C. finmarchicus* closely.

Maxilliped (figure 8, i): coxopodite and basipodite similar to stage IV; endopodite five-jointed, first joint with five setae, second with three, third with two, fourth with two setae on inner margin and one on outer margin, fifth with four setae.

First Leg (figure 8, m): coxopodite and basipodite as in stage IV; endopodite and exopodite three-jointed; first joint of endopodite with one seta on inner margin, second with two setae on inner margin, third with six setae, three on inner margin, two terminal and one on outer margin; first joint of exopodite with one seta on inner margin, a long slender spine on distal margin as in stage IV, second joint similar to first, third joint with three setae on inner margin, two terminal setae, one slender terminal spine and one slender spine on outer margin; first leg now similar to adult stage. Lebour's figure for *C. finmarchicus* does not show seta on basipodite; spines of exopodite short and stout; gulf of Maine specimens resembled *C. tonsus* closely.

Second Leg (figure 9, b): coxopodite and basipodite as in stage IV; endopodite and exopodite three-jointed; first joint of endopodite with one seta on inner margin, finely setose on outer margin as in stage IV, second joint with two setae on inner margin, finely setose on outer margin which is projected into a distal spine, third joint with eight setae, four on inner margin, two terminal and two on outer margin which is finely setose proximally; first joint of exopodite as in stage IV, second joint resembling first and finely setose on outer margin, third

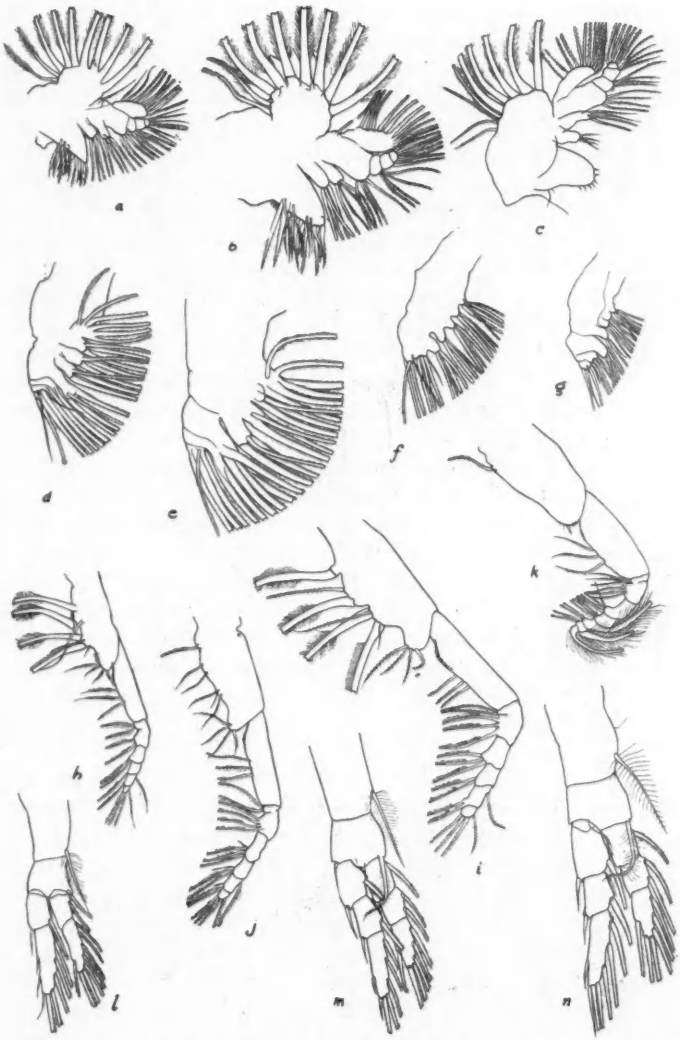

FIGURE 8. *Calanus tonsus* Brady. Copepodid stages x 27.8. IV, first maxilla,—a, second maxilla,—d, maxilliped,—h, first leg,—l; V, first maxilla,—b, second maxilla—e, maxilliped,—i, first leg,—m; VI, first maxilla ♀,—c, second maxilla ♀,—f, ♂—g, maxilliped ♀,—j, ♂—k, first leg,—n.

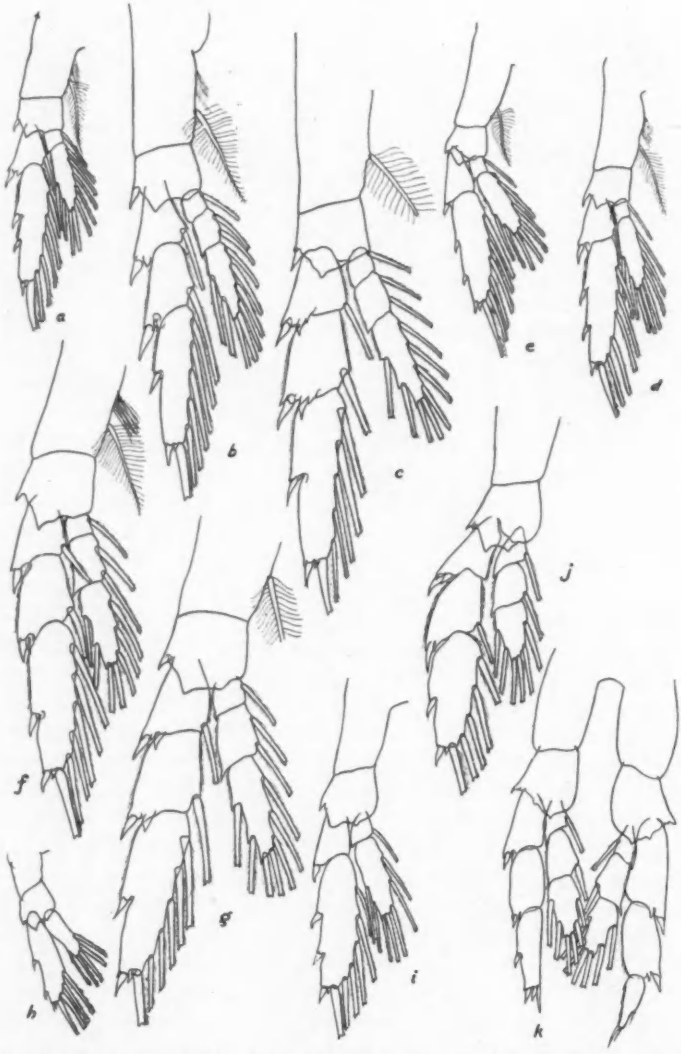

FIGURE 9. *Calanus tonsus* Brady. Copepodid stages x 27.8. IV, second leg,—a, third leg, —d, fourth leg,—e, fifth leg,—h; V, second leg,—b, fourth leg,—f, fifth leg —i; VI ♀, second leg,—c, fourth leg,—g, fifth leg,—j; VI ♂, fifth leg,—k.

joint with five setae on inner margin, a terminal blade, two short terminal spines and one short spine on outer setose margin; appendage now like that of adult; very similar to that described by Lebour for *C. finmarchicus,* but joints of exopodite more slender in *C. tonsus* and spines on outer margin of terminal joint more proximally situated than in *C. finmarchicus.*

Third Leg (figure 9, f): coxopodite similar to stage IV, additional fine setae on inner margin, spine on basipodite now curved, more elongated; endopodite and exopodite three-jointed; first joint of endopodite bears one seta on inner margin, second with two setae on inner margin and distal outer setose margin produced to a sharp point; third joint with seven setae, three on inner margin, two terminal, two on outer margin, proximal outer margin finely setose; first joint of exopodite similar to stage IV, second joint resembles first, third joint with five setae on inner margin, a terminal blade, two short terminal spines and one short spine on outer margin which is finely setose proximally; appendage now as in stage VI. Lebour describes *C. finmarchicus* with eight setae on terminal joint of endopodite; seven present in gulf of Maine specimens examined as in *C. tonsus.*

Fourth Leg: appendage similar to third leg; fine hairs on inner margin of coxopodite absent.

Fifth Leg (figure 9, i): coxopodite and basipodite as in stage IV; endopodite and exopodite two-jointed; first joint of endopodite with one seta on inner margin, outer margin produced to a point; second joint bears seven setae, three on inner margin, two terminal, two on outer margin; first joint of exopodite with short curved spine on distal outer margin, second joint with five setae on inner margin, a terminal blade, two short terminal spines and two short spines on outer margin. In *C. finmarchicus* a row of teeth on inner margin of coxopodite; these never developed in *C. tonsus* and their absence is an important specific character. Second joint of endopodite bears only six setae in *C. finmarchicus* compared with seven in *C. tonsus.*

COPEPODID STAGE VI ♀ (figure 7, c)

Length 4.5 to 5.0 mm.; body stouter; first abdominal segment large and tumid. Attainment of maturity accompanied by considerable degeneration in mouth parts to be considered in greater detail later in discussion of life history. Second abdominal segment smaller than in stage V, still slightly longer than either third or fourth joints; five pairs swimming legs, three-jointed. Mature females frequently observed with two spermatophores attached to genital opening; eggs observed within body to number of two hundred or more. Mature female described by Brady as 3.6 mm. in length, considerably smaller than specimens observed from strait of Georgia.

First Antenna (figure 7, c): appendage twenty-five jointed extending posterior to tip of abdomen. Described by Brady as almost completely devoid of setae; Giesbrecht (1892) suggests that absence of such setae due to imperfect preservation of specimens; setae fairly conspicuous in specimens from British Columbia waters.

Second Antenna (figure 7, g): appendage similar to stage V; setae of basipodite reduced; setae on first and second joint of exopodite finer, more thread-like, setae of third to sixth joints coarser. Reduction in size of setae not characteristic of *C. finmarchicus*.

Mandible (figure 7, k): appendage considerably modified, masticatory edge of coxopodite absent, surface smooth; endopodite and exopodite similar to stage V. Toothed edge of coxopodite persists in adult of *C. finmarchicus*.

First Maxilla (figure 8, c): gnathobase almost completely devoid of armature of spike-like bristles, vestiges of some still indicated; setae of small lobe adjacent to gnathobase much reduced, shorter than those of second small lobe; external lobe of coxopodite with nine large setae, four less coarse than others; second joint of endopodite with four setae and six terminal setae; exopodite with eleven setae. First maxilla of *C. finmarchicus* similar to *C. tonsus* but armature of gnathobase persists; seven terminal setae on endopodite.

Second Maxilla (figure 8, f): appendage reduced in size; first lobe of coxopodite with only five setae, numbers of setae on remaining lobes same as on first lobe but setae finer. No such modification of second maxilla in *C. finmarchicus*.

Maxilliped (figure 8, j): appendage slightly smaller than in stage V; armature of coxopodite much reduced, four coarse setae represented now by very fine short setae similar to those on distal elevation of joint; first joint of endopodite now bears six setae, joint two with four setae, joint three with three setae, proximal seta very small in each case. Joint four bears two long and one very short setae on inner border and one long seta on outer border. Appendage resembles that of *C. finmarchicus*; setae of coxopodite more reduced in *C. tonsus*.

First Leg (figure 8, n): appendage as in stage V; joints of appendage broader in *C. tonsus* than in *C. finmarchicus*.

Second Leg (figure 9, c): appendage similar to stage V; outer margin of third joint of endopodite with sharp projections at points of insertion of setae. In *C. finmarchicus* only seven figured by Sars on terminal joint of endopodite; eight setae indicated by Lebour as found in gulf of Maine specimens.

Third Leg (figure 9, g): similar to stage V; outer margin of second joint of endopodite finely setose; inner and outer margins of second joint of exopodite finely setose, proximal outer margin of exopodite with fine hairs. Third leg of *C. finmarchicus* figured by Lebour with eight setae on terminal joint of endopodite; only seven indicated by Sars as found in *C. tonsus*; gulf of Maine specimens agreed with Lebour's description.

Fourth Leg (figure 9, g): appendage as in stage V.

Fifth Leg (figure 9, j): endopodite and exopodite now three-jointed; first joint of endopodite with one seta on inner margin; second joint with one seta on inner margin, finely setose on outer margin, distal border projected into spine-like point; third joint broad at base, tapering distally with six setae, two on inner margin, two terminal, two on outer margin; first joint of exopodite finely setose on inner margin with three spines on distal outer margin; second joint finely setose with one seta on inner margin, three spines on distal outer margin which is

finely setose; third joint finely setose proximally, with four setae on inner margin, a terminal blade, two short terminal spines and one short spine on outer margin. Compared with *C. finmarchicus*, the fifth leg of *C. tonsus* is noticeably different in absence of teeth on coxopodite; joints broader, those of exopodite exhibiting definite convex curvature on outer margins; six setae on terminal joint of endopodite compared with five in *C. finmarchicus*.

COPEPODID STAGE VI ♂ (figure 7, d)

Length 4.6 mm. Five thoracic segments as in female, first smaller, approximately same size as following segments; abdomen five-jointed, longer than in female, second segment longer than any other, caudal rami as long as anal segment, spread outwards forming obtuse angles with posterior border of anal segment.

First Antenna (figure 7, d): appendage twenty-five jointed as in female, basal joints enlarged, terminal joints smaller; aesthetascs conspicuous along dorsal border.

Second Antenna (figure 7, h): appendage somewhat modified in male; basipodite larger, endopodite and exopodite slightly shorter; longer seta of basipodite extends past middle of first joint of endopodite; terminal joint of endopodite with only seven setae on inner margin and six apical setae; two fine thread-like setae absent, terminal seta nearest outer border coarser than in female, outermost with long hairs at right angles to long axis of seta; first joint of exopodite shorter than in female, arched on inner margin; setae of third to sixth joints exceptionally large. In *C. finmarchicus* antenna only very slightly modified; modification not indicated by Sars or Lebour.

Mandible (figure 7, l): masticatory edge of coxopodite absent as in female; setae on inner margin of basipodite reduced, additional seta on proximal outer margin of joint; first joint of endopodite convex on inner margin with one fairly long seta and vestiges of other three setae, outer margin of joint finely setose; second joint broader distally with nine setae, setae coarser and two slender thread-like setae absent, setae increasing in size toward outer setose border of joint; exopodite similar to that of female, joints slightly broader. Toothed edge of mandible persists in *C. finmarchicus*.

First Maxilla (figure 8, c): appendage similar to that of female but all vestiges of armature of gnathobase completely disappeared, only two setae on adjacent small lobe; second joint of endopodite with four setae, terminal joint with six setae.

Second Maxilla (figure 8, g): appendage much smaller than in female; first joint with only four setae, other lobes similar but setae smaller. No such reduction in *C. finmarchicus*.

Maxilliped (figure 8, k): appendage much modified; coxopodite practically smooth, free from setae with exception of one proximal seta, a short spine-like distal seta and few short spines; basipodite approximately same length as in female, broader, number of setae same; first joint of endopodite as in female,

second joint with lateral distal elevation and four equal setae, third joint broader than long with three equal setae and one very short seta, fourth joint short and broad with two equal and one much shorter seta on inner margin, outer seta very strongly developed, heavily plumose, directed posteriorly; fifth joint with two equal setae on inner margin, a coarsely plumose large terminal seta and similar large seta on outer margin. In *C. finmarchicus* endopodite modified as in *C. tonsus* but setae of coxopodite persist.

First, second, third and *fourth legs* similar to those in female.

Fifth Leg (figure 9, k): considerable modification, right and left legs dissimilar; coxopodite and basipodite of right and left legs same, resembling those of fifth legs of female; endopodite of each leg same, resembling that of female, joints slightly more elongated; in right leg, first joint of exopodite much like that of female, second joint narrower, lacking seta and fine hairs on inner margin and convex curvature, terminal joint more modified than others, slender, with one seta on inner margin, three terminal spines and one spine on outer margin; in left leg, first joint of exopodite larger than that of right leg, finely setose on inner margin, second joint slightly larger than that of right leg, finely setose on inner margin; terminal joint much smaller than in right leg, pear-shaped, tapering with minute hairs along inner surface, two slender terminal spines and one slender spine on outer margin. Joints comparatively stouter and broader than in *C. finmarchicus* with exception of terminal joint of exopodite of left leg which tapers sharply.

Euchaeta japonica Marukawa

Euchaeta japonica in the strait of Georgia is not an abundant species but always appears conspicuous in the hauls due to its large size and vivid colouring of red, white and blue. The mature specimens are rarely found above two hundred metres and occur in greatest numbers below that level where the temperature averages 8.8°C., and the salinity 17.4 gm. Cl. per litre.

Only two nauplius stages of *E. japonica* were obtained by artificial rearing in the laboratory, but the complete series of twelve developmental stages have been recognized and isolated from the plankton collections.

Mature females with their conspicuous blue egg sacs characterized the plankton throughout the year.

Nauplii appeared frequently in July, August, September and October but were also noted in January, March and again in May. In a sample collected July 15 at 400 to 200 metres, nauplii and several of the young copepodid stages were observed; the species appeared to be breeding in the 400 to 200 metre stratum. In the hauls taken during September and December, the majority of the specimens were males and females of the fifth and sixth copepodid stages, while the younger stages were not so conspicuous. In November, December and January and again in March, the hauls contained copepodid stages and in May, stages II and III were of frequent occurrence.

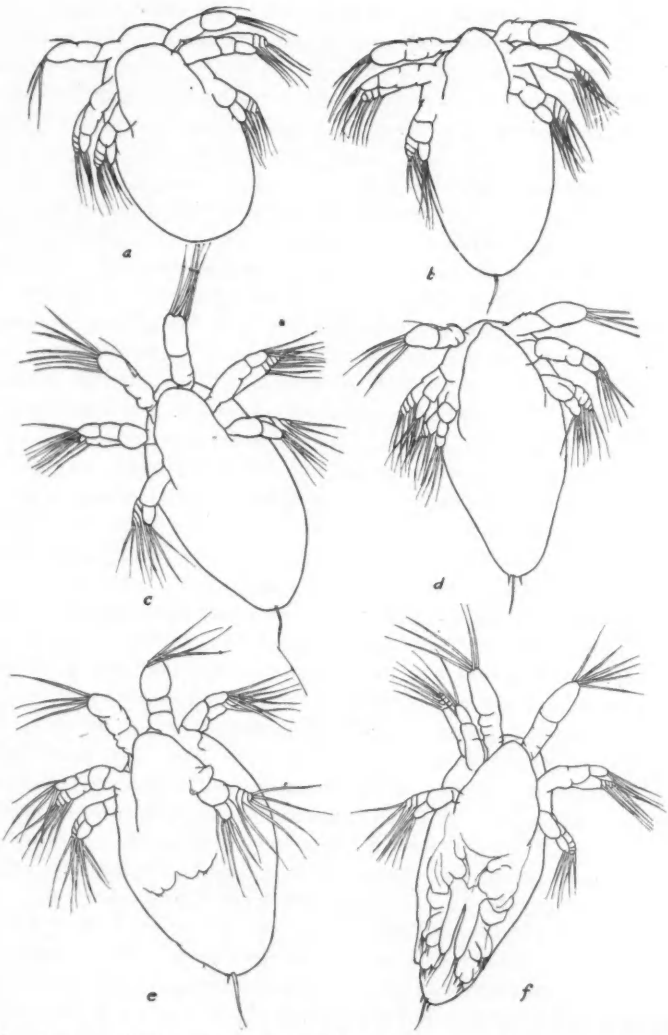

FIGURE 10. *Euchaeta japonica* Marukawa. Nauplius stages x 44. I,—a; II,—b; III,—c; IV,—d; V,—e; VI,—f.

Specimens of the different stages were mounted and examined as described for *C. tonsus*. The following descriptions are of the stages as taken from plankton samples with the exception of nauplius stages I and II which were reared in the laboratory. Each nauplius stage is compared with the same stage of *Euchaeta norvegica* Boeck as described by Nicholls (1934). The copepodid stages are compared with those of *E. norvegica* as observed by the writer from the gulf of Maine and described by Nicholls.

NAUPLIUS STAGE I (figure 10, a)

Length 0.59 mm. Body broadly oval, retaining blue colour of egg with larger and smaller drops of rose-coloured oil showing; three pairs of appendages developed, labrum conspicuous on ventral surface; eye noticeable anteriorly. Nauplius differs conspicuously from that of *Calanus tonsus*; larger, more smoothly oval in shape, appendages smaller in comparison with body, concentrated toward anterior end; very slight increase in size to be observed in following descriptions of nauplius I to nauplius VI; thorax not definitely differentiated from abdomen until quite late in development. *E. norvegica* described as 0.55 mm. long at this stage.

First Antenna (figure 11, a): three-jointed, uniramous; first joint short, broad, unarmed; second joint twice as long as wide, partially divided into three parts, two proximal lobes each with one short slender seta on ventral margin, distal lobe with long, coarse seta on ventral margin; terminal joint rounded at tip, twice as long as broad with three terminal setae, one slightly larger than others. This appendage is very similar in *E. norvegica.*

Second Antenna (figure 11, g): coxopodite and basipodite indicated as two lobes, imperfectly separated; endopodite incompletely separated from basipodite, two-jointed, first joint with one short fine seta on distal inner margin, terminal joint broadly rectangular in shape with one slender seta on inner margin and two large terminal plumose setae; exopodite five-jointed, first joint twice as long as broad, imperfectly separated from second with one large plumose seta on inner margin, second to fourth joints each with one large seta on distal inner margin, fifth joint with two terminal setae. In *E. norvegica* endopodite considered as unsegmented; additional seta on basipodite.

Mandible (figure 12, a): coxopodite one-jointed, unarmed; basipodite large broad joint with one short curved spine-like seta on inner elevation; endopodite one-jointed, broadly rectangular with two slight elevations on inner margin, each with one slender spine-like seta and two large terminal setae; exopodite four-jointed, first joint larger than others, quadrate; first, second and third joints each with one large plumose seta on inner margin, fourth or terminal joint with one large and one smaller plumose seta. Appendages resemble those of *C. tonsus* fairly closely, more robust with less elongated joints and coarser setae. Appendage in *E. norvegica* very similar.

NAUPLIUS STAGE II (figure 10, b)

Length 0.63 to 0.65 mm. Body with one slender feeler at posterior end;

three pairs appendages slightly more developed. *E. norvegica* smaller, 0.60 mm. long and with two posterior feelers.

First Antenna (figure 11, b): appendage slightly more elongated, terminal joint broader with four terminal plumose setae. Additional small spines on dorsal border in *E. norvegica.*

Second Antenna (figure 11, h): appendage similar to stage I, joints broader, setae slightly coarser; very short spine-like seta indicated on inner margin of basipodite; terminal joint of endopodite with three large terminal setae, slender seta on inner margin coarser, longer; exopodite with additional short fine seta on first joint. In *E. norvegica* an additional short seta on endopodite.

Mandible (figure 12, b): coxopodite similar to stage I, basipodite quadrate; endopodite bears one short fine seta on proximal inner margin, one large seta on distal inner margin and three large terminal setae; exopodite as in stage I. In *E. norvegica* an additional seta on first joint of exopodite.

NAUPLIUS STAGE III (figure 10, c)

Length 0.64 to 0.67 mm. Body elongated, labrum more conspicuous, three pairs of appendages as in earlier stages.

First Antenna (figure 11, c): first and second joints as in stages I and II; terminal joint now bears a very small spine-like seta on distal ventral border of joint, two short spine-like setae and two larger setae on distal dorsal border of joint, three large, coarse setae and one slender seta terminally. In *E. norvegica* setae on dorsal border of terminal joint very short, not plumose.

Second Antenna (figure 11, i): coxopodite and basipodite as in stage II; endopodite definitely separated from basipodite; first joint as in stage II, second joint with three large terminal setae, one large and one very fine seta on inner margin; exopodite as in stage II but terminal joint now bears two large setae and one short spine-like seta. In *E. norvegica* very similar but endopodite considered as unsegmented.

Mandible (figure 12, c): coxopodite and basipodite similar to stage II; endopodite elongated with a short fine seta half way along inner margin of joint, a large seta toward distal end and three large terminal setae; first joint of exopodite now bears an additional slender seta on inner margin, remaining joints as in stage II.

NAUPLIUS STAGE IV (figure 10, d)

Length 0.69 mm. Posterior portion of body narrower with one long seta and two short spines; three pairs of appendages slightly more developed than in stage III, no indication of first maxillae.

First Antenna (figure 11, d): terminal joint more elongated with additional very short spine-like seta on ventral border; short dorsal setae of stage III now long and coarse, a fifth short seta indicated proximal to these. In *E. norvegica,* two more proximal dorsal setae short, not plumose.

Second Antenna (figure 11, j): coxopodite, basipodite and endopodite un-

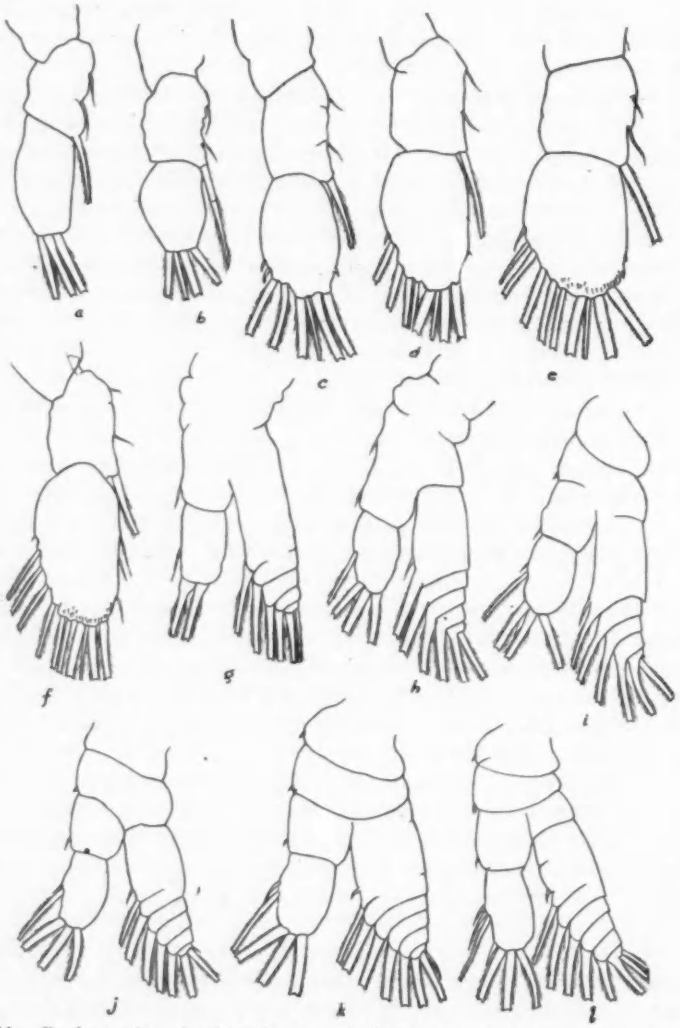

FIGURE 11. *Euchaeta japonica* Marukawa. Nuplius stages x 122.2. I, first antenna,—a, second antenna,—g; II, first antenna,—b, second antenna,—h; III, first antenna,—c, second antenna,—i; IV, first antenna,—d, second antenna,—j; V, first antenna,—e, second antenna,—k; VI, first antenna,—f, second antenna,—l.

changed; exopodite six-jointed, first joint with one short and one long seta; joints two to five each with one coarse seta, sixth joint with two long and one very short terminal setae. In *E. norvegica* one less seta on exopodite.

Mandible (figure 12, d): indication of two short spines on inner margin of coxopodite; basipodite unchanged; short seta on inner margin of endopodite now larger and coarser.

NAUPLIUS STAGE V (figure 10, e)

Length 0.8 mm. First antennae, second antennae and mandible further developed than in stage IV, first maxillae indicated as small bilobed structures posterior to mandibles; posterior end of body with one long seta and two short spines. *E. norvegica* described as 0.73 mm. long at this stage.

First Antenna (figure 11, e): terminal joint with five seta on dorsal margin, short slender seta proximal to these; two setae indicated on distal ventral margin, a row of small spines extending transversely across distal border of joint. In *E. norvegica* proximal dorsal seta not so well developed, only one ventral seta indicated.

Second Antenna (figure 11, k): appendage similar to stage IV, third terminal seta of exopodite now slightly longer.

Mandible (figure 12, e): appendage similar to stage IV.

First Maxilla (figure 12, g): first maxilla indicated as small bilobed appendage; inner lobe unarmed, distinct from outer lobe bearing three short setae. No description given by Nicholls (1934) for this appendage of *E. norvegica.*

NAUPLIUS STAGE VI (figure 10, f)

Length 0.83 to 0.90 mm. Body more elongated, tapered posteriorly; first and second maxillae well developed; maxillipeds indicated as elongated lobes on middle line; first and second pairs swimming legs evident as bilobed structures toward posterior end. Here is a retarded development of appendages as compared with *C. tonsus*; maxillae and maxillipeds evident as setose lobes of indefinite structure, but are well developed, segmented appendages in *C. tonsus. E. norvegica* described as 0.78 mm. long at this stage. First and second legs not yet developed.

First Antenna (figure 11, f): terminal joint now bears three slender setae on ventral margin, four terminal setae, six setae on dorsal margin and an indication of short spine-like seta. In *E. norvegica* terminal joint slightly less elongated.

Second Antenna (figure 11, l): coxopodite with short spine-like seta on inner margin; basipodite with two short spine-like setae; first joint of endopodite as in earlier stages, second joint with one long and two shorter setae on inner margin, three long and one short terminal setae; exopodite seven-jointed, first joint short, imperfectly divided from second, second with one short spine-like seta and one long seta, third to sixth joints each with one long seta, terminal joint with one coarse and two slender terminal setae. *E. norvegica* very similar, additional short seta on outer border of exopodite.

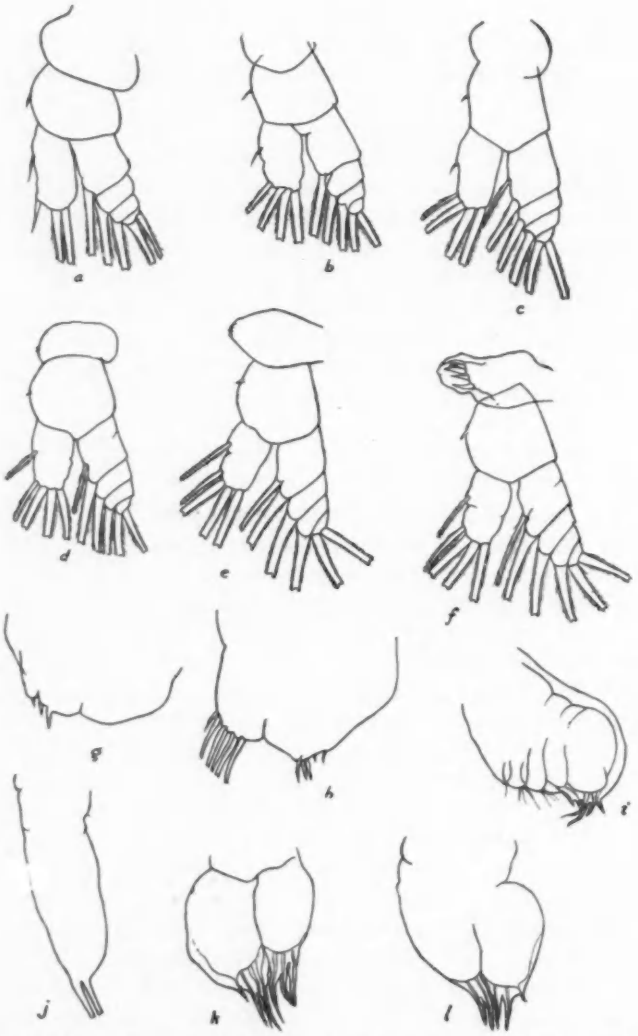

FIGURE 12. *Euchaeta japonica* Marukawa. Nauplius stages x 122.2. I, mandible,—a; II, VI, mandible,—f, first maxilla,—h, second maxilla,—i, maxilliped,—j, first leg,—k, second leg,—l.

Mandible (figure 12, f): definite teeth indicated along masticatory edge of coxopodite; basipodite with additional short spine indicated on inner margin; indication of two joints in endopodite, number of setae same; more definite division of first joint of exopodite into two portions. In *E. norvegica,* teeth on coxopodite not indicated.

First Maxilla (figure 12, h): inner lobe now bears three short terminal setae and two short setae on inner margin, outer lobe or exopodite with five long and one shorter setae. Appendage very similar in *E. norvegica.*

Second Maxilla (figure 12, i): imperfectly divided into lobes; setae difficult to distinguish; each of proximal lobes with about three very short fine setae, terminal portion with seven fine setae. Appendage not figured by Nicholls (1934) for *E. norvegica.*

Maxilliped (figure 12, j): appendage an elongated lobe with two large terminal setae; indications of additional lateral setae beneath chitin. Three terminal setae in *E. norvegica.*

First Leg (figure 12, k): coxopodite and basipodite undifferentiated; endopodite oval with three terminal setae; exopodite larger, broader with three equal terminal setae and one shorter seta on distal outer border.

Second Leg (figure 12, l): appendage similar to first leg, not as far developed; endopodite and exopodite subequal; endopodite bears two terminal setae; exopodite with two terminal and one short spine-like seta on outer distal margin.

COPEPODID STAGE I (figure 13, a)

Length 1.2 mm. General shape of body resembles adult, broader in comparison with length; three free thoracic segments; abdomen two-jointed, second joint longer than first; caudal furca longer in comparison to those in adult, three similar caudal setae and one appendicular bristle; body transparent white with conspicuous drops of rose-coloured oil in dorsal region of thorax; two pairs swimming legs well developed, indication of third pair. Transition from sixth nauplius to first copepodid stage accompanied by marked change in shape as previously described for *Calanus tonsus. E. norvegica* very similar in general appearance at this stage.

First Antenna (figure 13, a): ten-jointed; fourth joint almost twice as long as second or third, terminal joint slightly longer than fourth; second, third, fourth, fifth, sixth and terminal joints each with long setae. In *E. norvegica* appendage described as nine-jointed.

Second Antenna (figure 13, d): coxopodite bears one plumose seta on inner margin, basipodite large, quadrate, with two slender setae on inner margin; first joint of endopodite longer than second with two slender setae on inner margin toward distal end; setae of terminal joint originate nearer distal end, three on inner margin, five equal terminal setae; exopodite seven-jointed, first joint short, broad; second, quadrate with very fine seta on inner distal margin; third to sixth joints shortened, each with one long plumose seta on inner margin; seventh joint longer than second, narrower, with one slender lateral seta and three equal terminal plumose setae. A rearrangement of setae evident here as in *C. tonsus;*

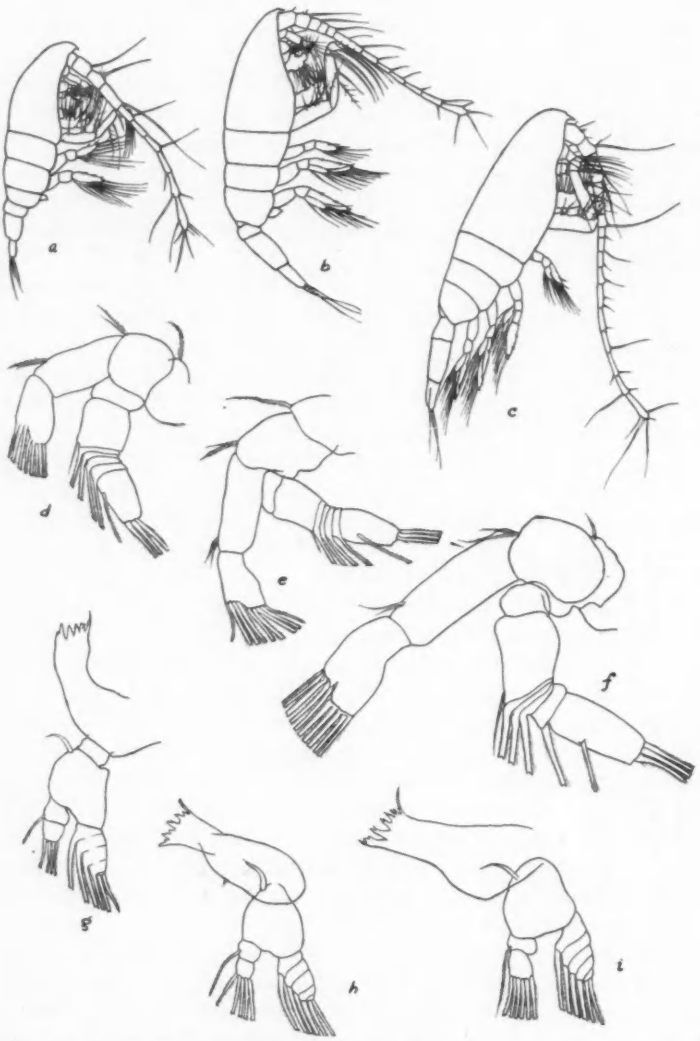

FIGURE 13. *Euchaeta japonica* Marukawa. Copepodid stages. I, whole animal x 10,—a, second antenna x 44,—d, mandible x 44,—g; II, whole animal x 10,—b, second antenna x 44,—e, mandible x 44,—h; III, whole animal x 10,—c, second antenna x 44,—f, mandible x 44,—i.

marked tendency for some of the joints to telescope into each other. In *E. norvegica* inner terminal seta of endopodite shorter and finer than others. Only three setae observed on inner margin of endopodite in specimens from gulf of Maine but Nicholls (1934) described four.

Mandible (figure 13, g): coxopodite considerably enlarged with conspicuous toothed process, two outermost teeth strong, blunter than others, short plumose seta on inner margin, basipodite with short smooth, stout seta on inner proximal margin; endopodite two-jointed; first joint with one plumose seta on inner distal margin, slightly convex on outer margin, second joint with four long equal setae less coarse than in nauplius VI; exopodite five-jointed, first four joints each with one large plumose seta, smaller terminal joint with two slender plumose setae. Appendage very similar in *E. norvegica.*

First Maxilla (figure 14, a): appendage considerably modified; coxopodite with one large and one very small internal lobe, a flattened external lobe or elevation; large internal lobe or gnathobase armed with five spike-like bristles and four more slender plumose bristles; other internal lobe very small, deeply set between gnathobase and endopodite—it bears one long, slender plumose seta. External elevation or epipodite bears four equal plumose setae; endopodite three-jointed, first joint large with one long plumose seta, second joint smaller, imperfectly divided from the third with one long and one shorter plumose seta, terminal joint with three setae, one shorter and smooth, others finely toothed; exopodite with seven long plumose setae. Appendage noticeably different from *C. tonsus* in the absence of two oval internal lobes between gnathobase and endopodite. In *E. norvegica* epipodite bears only three setae, one long, two much shorter in specimens from gulf of Maine, but Nicholls indicates only two setae; endopodite with eight setae, coxopodite with two small internal lobes.

Second Maxilla (figure 14, d): appendage definitely divided into lobes; coxopodite with three equal proximal lobes and slightly larger distal lobe; first lobe bears two long coarsely plumose setae and one very short stumpy seta, second to fourth lobes similar in armature, each with two long coarsely plumose setae and one shorter seta with fine lateral spikes; basipodite imperfectly divided from coxopodite, with one long coarsely plumose seta, one shorter spine-like seta and one short seta with lateral spines; endopodite or terminal portion bears five setae, two with lateral spines and three coarsely plumose. In *E. norvegica* setae of coxopodite further developed and endopodite with eight setae (Nicholls).

Maxilliped (figure 14, g): coxopodite rectangular with five coarse setae, thickened at base, armed with lateral spikes, one toward proximal end of joint, two about half way along, two at distal end and cluster of five spines at base of first of two middle setae; basipodite same size as coxopodite, directed at right angles to it, bears two setae, one with lateral spines and one finely setose; endopodite incompletely divided into three joints; first bears a short smooth spine-like bristle, second with one long claw-like spine, terminal joint with four claw-like spines. In *E. norvegica* no short smooth bristle on first joint of endopodite.

First Leg (figure 15, a): coxopodite and basipodite differentiated, one-

jointed; endopodite with five plumose setae, three on inner margin and two terminal; exopodite unsegmented with two long setae on inner margin, two terminal setae, one short smooth terminal spine, one finely setose, longer terminal spine and a similar setose spine on outer margin. In *E. norvegica* two spines on outer margin of exopodite, this additional spine a specific character constant throughout later stages. Nicholls describes exopodite with five plumose setae in this stage and later in II and III. In gulf of Maine specimens one of these setae is spinous.

Second Leg (figure 15, d): coxopodite and basipodite each one-jointed unarmed; endopodite more elongated than in first leg, unsegmented with six plumose setae, three on inner margin, two terminal, one on outer margin; exopodite unsegmented, with three setae on inner margin, a terminal spine, one short smooth terminal spine, one short finely setose terminal spine and two similar setose spines on outer margin. Short smooth terminal spine between terminal blade and short finely setose spine of exopodite not indicated for *E. norvegica*.

COPEPODID STAGE II (figure 13, b)

Length 1.0 mm. Three free thoracic segments; two abdominal segments, second joint very long; caudal furca longer than in stage I, setae similar; eye conspicuous, red; large drop of salmon pink oil placed dorsally; three pairs swimming legs well developed, fourth pair indicated. Specimens of *E. norvegica* averaged 1.6 to 1.8 mm., very similar.

First Antenna (figure 13, b): twelve-jointed, extending to end of thorax; third joint imperfectly divided into two, sixth into four parts. Nicholls considers appendage as fourteen-jointed in *E. norvegica*.

Second Antenna (figure 13, e): coxopodite and basipodite as in stage I; first joint of endopodite almost double length of terminal joint which now bears four setae on distal inner margin and five terminal plumose setae; second and seventh joints of exopodite elongated.

Mandible (figure 13, h): appendage similar to stage I; teeth on coxopodite more numerous, five terminal setae on second joint of endopodite.

First Maxilla (figure 14, b): gnathobase with five spike-like bristles, five plumose setae; epipodite with five long setae; first joint of endopodite with short fine seta and long coarse seta, second joint unchanged, third joint with three setae; exopodite as in stage I. In *E. norvegica* exopodite bears a cluster of fine hairs on inner margin and epipodite bears but four setae. According to Nicholls, the gnathobase bears only nine setae and there are two small internal lobes of the coxopodite.

Second Maxilla (figure 14, e): short stumpy seta of first lobe of coxopodite now similar to those of other joints, bears lateral spines; endopodite bears additional short smooth spine.

Maxilliped (figure 14, h): coxopodite with slender plumose seta toward proximal outer border of joint, two spinous setae on proximal inner border, two distal setae, one spinous, one plumose; basipodite bears row of very fine spines

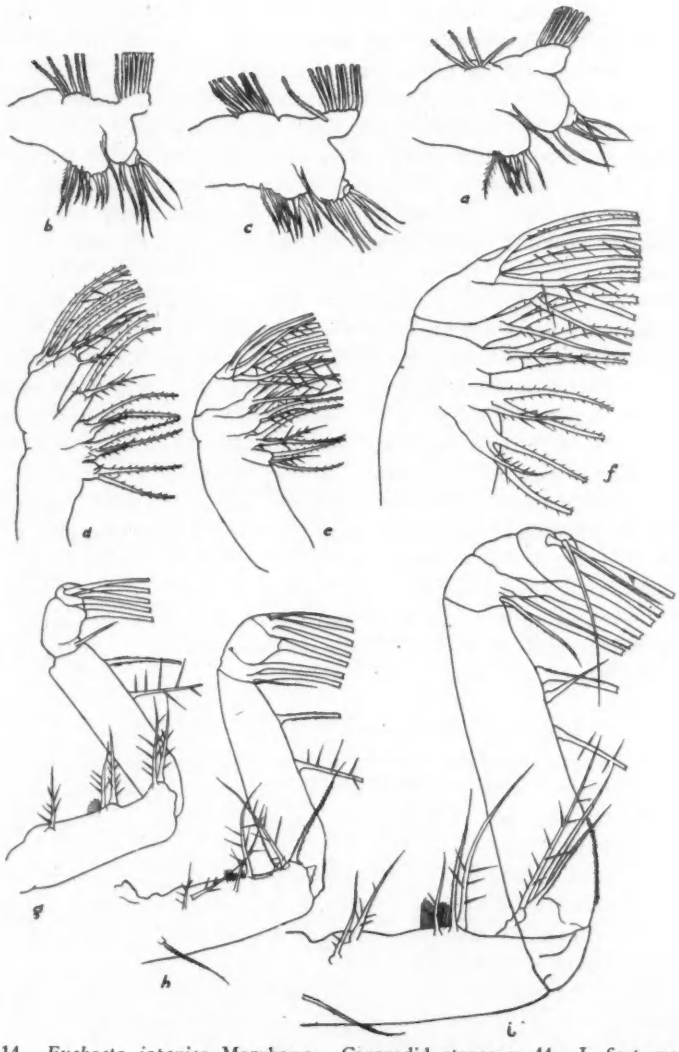

FIGURE 14. *Euchaeta japonica* Marukawa. Copepodid stages x 44. I, first maxilla,—a, second maxilla,—d, maxilliped,—g; II, first maxilla,—b, second maxilla,—e, maxilliped, —h; III, first maxilla,—c, second maxilla,—f, maxilliped,—i.

along proximal outer border; endopodite definitely divided into three joints, first with two long equal claw-like spines and one very fine plumose seta, second with one claw-like spine, terminal joint with three curved spines and one slender plumose bristle. In *E. norvegica,* only six setae on coxopodite, first seta of endopodite considered as part of basipodite (Nicholls).

First Leg (figure 15, b): coxopodite one-jointed with cluster of long fine hairs on inner margin; basipodite also finely setose on inner margin with one curved plumose seta on inner distal margin of joint; endopodite bears five setae as in stage I, slight indication of setose lobe on outer margin of joint; exopodite bears five setae, terminal and outer spines more elongated. In *E. norvegica* additional spine on proximal outer margin of exopodite and no seta on basipodite (Nicholls).

Second Leg (figure 15, e): coxopodite now bears tuft of fine hairs and one plumose seta on inner margin; basipodite as in stage I; endopodite one-jointed with five setae, more elongated; exopodite one-jointed with three setae on inner setose margin, one terminal seta, one terminal blade, short smooth terminal spine, a short finely setose terminal spine and two similar spines on outer margin. *E. norvegica* at this stage bears only five setae on endopodite (Nicholls 1934).

Third Leg (figure 15, g): coxopodite and basipodite each one-jointed, unarmed; endopodite unsegmented with six setae, one on proximal inner margin, two on distal inner margin, two terminal and one on outer margin; exopodite unsegmented, finely setose on inner proximal border with two setae on inner margin, one terminal seta, one terminal blade, one short smooth terminal spine, one short finely setose terminal spine and two similar spines on outer margin. Short smooth terminal spine of exopodite not indicated by Nicholls for *E. norvegica* in this stage or later stages.

COPEPODID STAGE III (figure 13, c)

Length 2.4 mm. Four pairs swimming legs well developed; eye conspicuous; considerable salmon pink oil in body cavity; bases of maxillipeds salmon pink, bases of other mouth parts faintly tinted. Specimens of *E. norvegica* similar in appearance and size.

First Antenna (figure 13, c): sixteen-jointed, extending to end of abdomen, third joint imperfectly divided into four. In *E. norvegica* third joint definitely divided into four parts as observed in specimens from gulf of Maine, but Nicholls described appendage as twenty-two jointed.

Second Antenna (figure 13, f): appendage similar to stage II, larger; setae on coxopodite reduced; second joint of endopodite now bears two groups of five setae each, innermost seta more slender than others.

Mandible (figure 13, i): outer margin of first joint of endopodite convexly rounded, second joint with six plumose terminal setae.

First Maxilla (figure 14, c): gnathobase with six spike-like bristles and four slightly longer plumose bristles; epipodite with seven long equal setae, one short stumpy seta, basal joint of endopodite with one large and two smaller setae,

numbers of setae same for second and third joints, terminal joint with few fine hairs on external margin; exopodite with eight setae. In *E. norvegica* the inner margin of exopodite is plumose, but appendage is similar as observed by the writer; Nicholls indicates only six setae on epipodite and ten setae on endopodite. With (1915) observed eight setae on exopodite of *E. norvegica.*

Second Maxilla (figure 14, f): basipodite with two finely toothed spine-like setae, one shorter spinous seta; terminal joint of endopodite with six setae, two with lateral spines, one coarsely plumose, three finely toothed claw-like spines. In *E. norvegica,* four of terminal setae described as finely toothed by Nicholls.

Maxilliped (figure 14, i): coxopodite bears two additional setae, both plumose, one situated in middle group, one in distal group of joint; basipodite bears additional short smooth seta between spinous and finely toothed setae described for stage II; endopodite four-jointed, first joint with two finely toothed claw-like spines and one slender plumose bristle, second joint with one spine, third with one spine and one slender plumose seta, terminal joint with two spines and one slender smooth bristle. In *E. norvegica,* coxopodite with only eight setae, endopodite three-jointed with an additional terminal seta (Nicholls).

First Leg (figure 15, c): endopodite bears definite outer lobe with curved row of short spines; exopodite more elongated, outer distal border finely setose. In *E. norvegica,* characteristic additional spine present on exopodite.

Second Leg (figure 15, f): coxopodite, basipodite and endopodite as in stage II, distal outer margin of latter finely setose, proximal border produced into spine; exopodite two-jointed, first joint with one slender plumose seta on inner setose margin, one short finely setose spine on distal outer margin, second joint with four setae on inner margin, one terminal seta, one terminal blade, one short smooth terminal spine, one short setose terminal spine and two setose spines on outer margin—more distal outer spine larger than proximal spine. As in earlier stages, no short smooth terminal spine on exopodite indicated by Nicholls for *E. norvegica.*

Third Leg (figure 15, h): coxopodite bears group of long fine hairs and plumose seta on inner margin; endopodite unsegmented, elongated with seven setae, four on inner margin, two terminal and one on outer margin; inner border of endopodite setose, proximal border slightly produced into spine; exopodite two-jointed, first joint finely setose on inner margin with one short setose spine on distal outer margin, second joint with three setae on inner margin which is finely setose proximally, one terminal seta, one terminal blade, one very short and one short smooth terminal spine, one short setose terminal spine and similar setose spine on outer margin. In *E. norvegica,* only six setae on endopodite but an additional spine on outer margin of terminal joint of exopodite (Nicholls).

Fourth Leg (figure 15, i): coxopodite and basipodite one-jointed, unarmed; endopodite unsegmented with six plumose setae, three on inner margin, two terminal and one on outer setose margin; exopodite unsegmented with two setae on inner setose margin, one terminal seta, one terminal blade, one short smooth terminal spine, one short setose terminal spine and two short setose spines on outer margin.

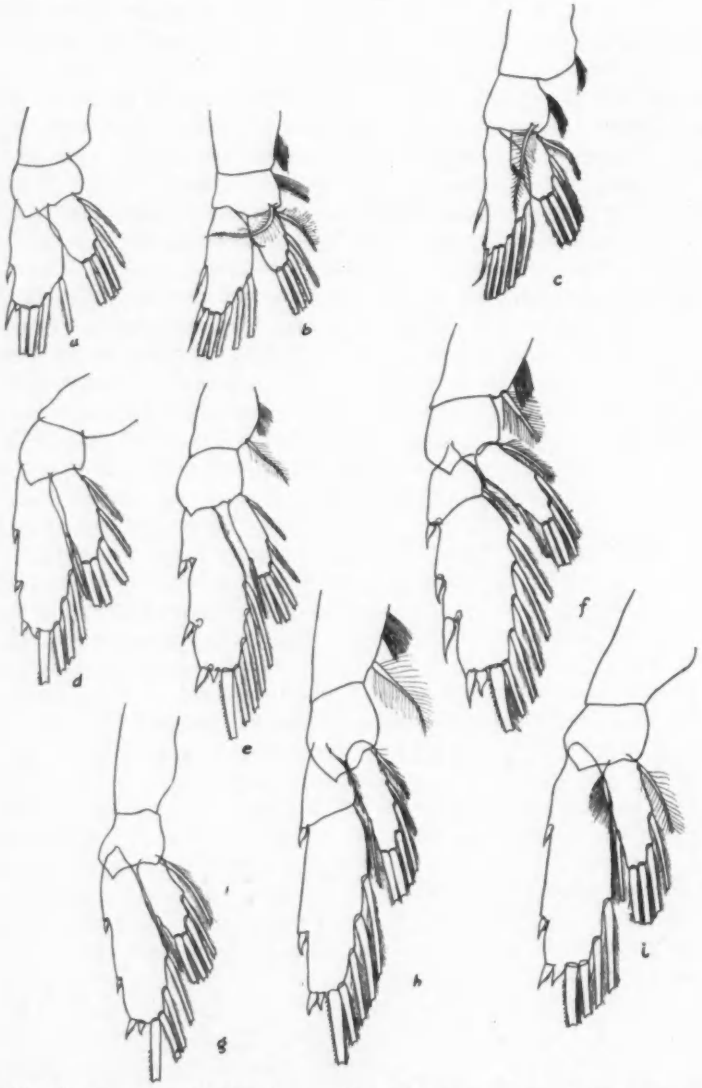

FIGURE 15. *Euchaeta japonica* Marukawa. Copepodid stages x 44. I, first leg,—a, second leg,—d; II, first leg,—b, second leg,—e, third leg,—g; III, first leg,—c, second leg,—f, third leg,—h, fourth leg,—i.

COPEPODID STAGE IV (figure 16, a)

Length, 4.2 mm. Three abdominal segments, first two equal and shorter than third; edges of thorax projected into points; males and females differentiated at this stage due to presence of small pair of fifth legs in former. Specimens of *E. norvegica* averaged 3.8 to 4.0 mm. in length.

First Antenna (figure 16, a): twenty-one jointed, ninth joint incompletely divided into three. In *E. norvegica* antenna twenty-three jointed as observed in specimens from gulf of Maine, but Nicholls describes appendage as twenty-four jointed.

Second Antenna (figure 16, f): terminal joints of endopodite with two groups of six setae each.

Mandible (figure 16, j): second joint now with seven terminal setae.

First Maxilla (figure 17, a): gnathobase now armed with eight spike-like bristles and four more slender plumose bristles; coxopodite now with two small internal lobes, each with one long slender plumose seta; first and third joints of endopodite unchanged, second now bears two long plumose setae and one short smooth seta; exopodite bears nine equal setae. In *E. norvegica* inner edge of exopodite bears a clump of fine hairs; endopodite with eleven setae according to Nicholls.

Second Maxilla (figure 17, e): six terminal setae, one with lateral spines, other five modified as finely toothed claw-like spines. In *E. norvegica* only four of terminal setae described as finely toothed (Nicholls).

Maxilliped (figure 17, i): number of setae on coxopodite same, some modified; one spinous seta in proximal group now finely toothed, only one of middle group now spinous, two finely toothed, three setae of distal group with no lateral spines; middle seta of basipodite longer, base thickened, tip narrowed, proximal seta of basipodite now finely toothed; inner margin bears row of fine spines toward distal end of joint; endopodite five-jointed, first joint bears three coarse spines, one slender bristle, second joint one coarse spine, fourth joint one coarse spine and one slender seta, terminal joint bears two spines, one slender bristle and one very short seta. In *E. norvegica* number of setae the same but endopodite considered as four-jointed (Nicholls).

First Leg (figure 17, m): distal outer margin of endopodite and inner margin of exopodite now finely setose. In *E. norvegica* additional spine on exopodite.

Second Leg (figure 18, a): similar to stage III.

Third Leg (figure 18, d): outer proximal margin of endopodite bears small pointed projection, some evidence of a division into two joints in male; exopodite two-jointed, first joint finely setose with plumose seta on inner margin, one short setose spine on distal outer margin, second joint with four setae on inner margin, a terminal seta, a terminal blade, one short smooth terminal spine, one short setose terminal spine, and two short setose spines on outer margin. In *E. norvegica* endopodite two-jointed in both males and females.

Fourth Leg (figure 18, e): coxopodite bears plumose seta on inner margin; endopodite two-jointed; first joint with seta on inner margin, second joint with six

setae, three on inner margin, two terminal setae, one on outer setose margin; exopodite two-jointed; first joint finely setose along inner margin with one short setose spine on outer distal margin, second joint finely setose along inner proximal margin with four setae on inner margin, one terminal seta, one terminal blade, one short smooth terminal spine, one short terminal setose spine and two setose spines on outer margin.

Fifth Legs of Male (figure 18, h): small mitten-shaped structures, similar; coxopodite of each leg one-jointed, unarmed; basipodite of each leg also one-jointed, smooth, that of right leg slightly larger; endopodite small, unsegmented, that of right leg slightly broader, one and a half times as long; exopodite of each leg unsegmented, three times as long as endopodite, tapering distally. In *E. norvegica* legs similar but endopodites tapering more sharply.

COPEPODID STAGE V ♀ (figure 16, b); V ♂ (figure 16, c)

Length 5.5 mm. Three free thoracic segments, four abdominal segments, subequal; females more robust than males but no fifth pair swimming legs developed, other appendages similar in both sexes. Females of *E. norvegica* average 5.5 mm. in length, males 5.1 to 5.8 mm.

First Antenna (figure 16, c): twenty-three jointed, basal joints quadrate, elongated terminal joints. Appendage twenty-four jointed in *E. norvegica.*

Second Antenna (figure 16, g): terminal joint of endopodite bears thirteen setae; innermost seta of inner group of seven shorter than others, six setae of outer group subequal; seta of second joint of exopodite finer in comparison to those of joints three to six, than in stage IV. Marukawa (1921) in original description of second antenna of male figured no seta on inner margin of coxopodite and only one seta on basipodite and first joint of endopodite; separation of joints three, four, five and six of exopodite not clearly indicated. The fine seta on second joint of exopodite not evident in male of *E. norvegica.*

Mandible (figure 16, k): second joint of endopodite now bears eight terminal setae.

First Maxilla (figure 17, b): gnathobase and epipodite as in stage IV; first joint of endopodite with one long, two short and one very short setae, second and third joints as in stage IV; exopodite with ten long setae. Marukawa's figure for this appendage of male at this stage not clear; gnathobase pictured as triangular lobe bearing two or three setae, lacking conspicuous spike-like bristles noted in the British Columbia specimens; two small internal lobes of coxopodite not indicated; epipodite bears nine setae; endopodite and exopodite as in British Columbia specimens. In *E. norvegica* gnathobase with thirteen setae, epipodite with nine and endopodite with thirteen setae (Nicholls).

Second Maxilla (figure 17, f): appendage as in stage IV, larger.

Maxilliped (figure 17, j): additional spines at base of second group of setae on coxopodite; first joint of endopodite with three spine-like setae and two slender plumose bristles, second and third joints each with one spine and one slender bristle, fourth joint with one spine, one large bristle and one slender plumose

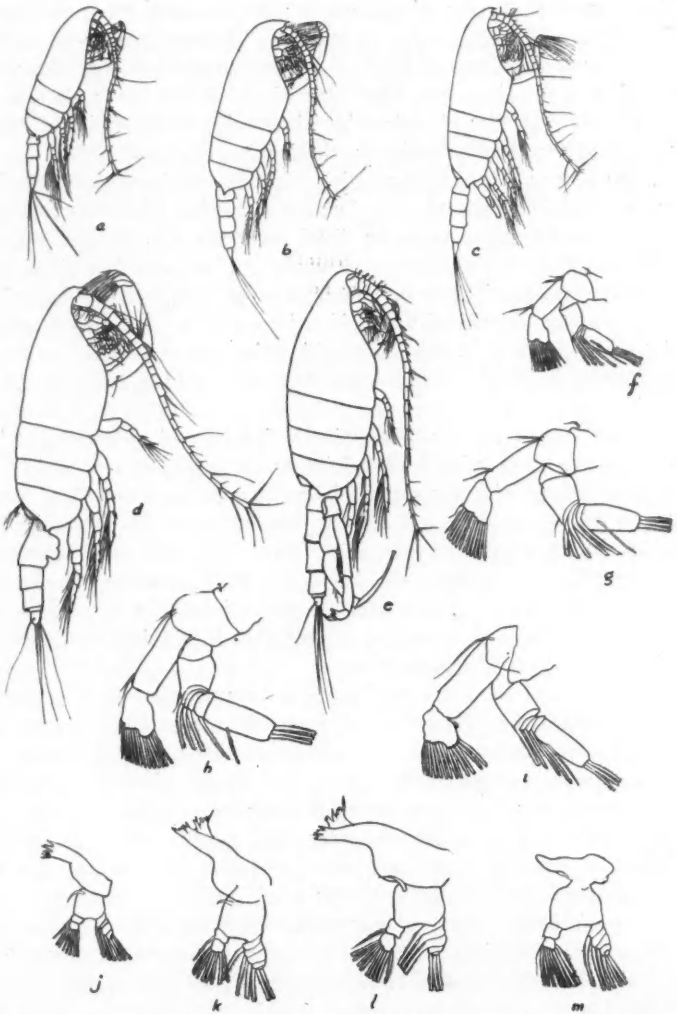

FIGURE 16. *Euchaeta japonica* Marukawa. Copepodid stages. IV, whole animal x 3.3,—a, second antenna x 16.6,—f, mandible x 16.6,—j; V, whole animal ♀,—b, ♂,—c, second antenna x 16.6,—g, mandible x 16.6,—k; VI ♀ whole animal x 3.3,—d, second antenna x 16.6,—h, mandible x 16.6,—l; VI ♂ whole animal x 3.3,—e, second antenna x 16.6, —i, mandible x 16.6,—m.

bristle, terminal joint with two spines, one long slender bristle and one very short fine seta. In Marukawa's figure for this appendage of male, only one spinous seta indicated on proximal border of coxopodite; the plumose seta noted in British Columbia specimens lacking; setae of middle and distal groups all pictured as smooth, but in specimens examined one of former group is spinous, others plumose. Marukawa figures the eight spine-like setae of endopodite, finer plumose bristles not indicated. Fine bristles of endopodite observed in specimens of *E. norvegica* examined by author; Nicholls indicates additional seta on endopodite.

First Leg (figure 17, n): coxopodite, basipodite and endopodite as in stage IV; exopodite two-jointed, first joint finely setose with one distal seta on inner margin and a slender setose spine on distal outer concave margin, second joint with three setae on inner margin, one terminal seta, one short terminal spine and one long slender setose spine; appendage now as in adult. In *E. norvegica* additional spine on outer margin of first joint of exopodite. Nicholls describes terminal joint with one spine at this stage—this spine was considered as a plumose seta in earlier stages. With (1915) describes exopodite of *E. norvegica* as unsegmented at this stage.

Second Leg (figure 18, b): coxopodite, basipodite and endopodite as in stage IV; exopodite now three-jointed, first joint as in stage IV, second joint larger than first, finely setose with one seta on inner margin; on outer distal margin of this joint, two spines, one short and smooth, one longer setose outer spine extending past middle of first spine of third joint; third joint with three setae on inner margin, one terminal seta, one terminal blade, one short smooth terminal spine and one short setose terminal spine; on outer margin of joint, two setose spines, distal spine larger. Short, smooth spines of second and third joints of exopodite not indicated in *E. norvegica* (Nicholls 1934).

Third Leg (figure 18, f): coxopodite and basipodite as in stage IV; endopodite and exopodite three-jointed; first joint of endopodite with one seta on inner margin, outer margin convex, produced to a point distally, second joint similar to first, outer margin finely setose with sharper distal projection, third joint with five setae, two on inner margin, two terminal and one on outer margin which is finely setose along proximal border; first joint of exopodite as in stage IV, second similar to first, larger, with short smooth spine in addition to longer setose spine on outer distal margin of joint; third joint with three setae on inner margin, one terminal seta, one terminal blade, one short smooth terminal spine, one short setose terminal spine, two short setose spines on outer margin; appendage now as in adult. Terminal joint of endopodite slightly more elongated and slender in *E. norvegica*.

Fourth Leg (figure 18, f): appendage similar to third leg, inner margin of coxopodite not finely setose.

Fifth Legs of Male (figure 18, i): right and left legs dissimilar; basipodite of right leg considerably larger, endopodite unsegmented, that of left leg scarcely half as long as that of right leg; exopodite of each leg one-jointed, left exopodite terminating bluntly with faint indication of two spines, is shorter than right exopo-

dite which bears one short blunt spine. Marukawa's description similar. Fifth legs of male of *E. norvegica* similar; left exopodite nearly as long as right (i.e., longer than in *E. japonica*), tapered to definite point with two fairly sharp projections on inner distal margin; endopodite more pointed than rounded distally; right exopodite tapers sharply toward distal end of joint.

COPEPODID STAGE VI ♀ (figure 16, d)

Length 6.3 mm. Three free thoracic segments; sides of last segment not broadly rounded but produced into conspicuous nodiform projections; dorsal ledge clothed with long fine hairs, lateral margins with shorter hairs; abdomen four-jointed, attaining less than half length of anterior part; genital segment very large, proximal part narrow, a large genital protuberance arising from middle of segment, extending obliquely behind; second and third abdominal segments subequal with posterior margins denticulate; anal segment shortened; caudal furca scarcely attain length of second or third segments. Mature specimens vividly coloured; body transparent white, bases of swimming legs and mouth parts vivid red, large drop of coloured oil dorsal to mouth parts, setae of caudal rami iridescent, eggs carried in a sac attached to genital segment, bright royal blue; two tentaculiferans *Ophryodendron* and *Trichophyra* frequently found on abdomen. Female is described by Marukawa as 8 mm. long; British Columbia specimens smaller, averaging 6.3 mm. *E. elongata* Esterly considerably smaller, 4.13 mm., *E. norvegica* larger, 7.5 to 7.8 mm. Appendages and thoracic projections of *E. elongata* similar to those of *E. japonica* but rostral ledge and tufts of hair on thorax absent. In *E. norvegica* sides of last thoracic segment broadly rounded, finely setose, but lack dorsal tuft of long hairs so characteristic of *E. japonica*. Number of eggs in egg sac of *E. norvegica* averages 28 to 30 as compared with 17 to 18 in *E. japonica*.

First Antenna (figure 16, d) : twenty-four jointed, scarcely extending to distal end of genital segment.

Second Antenna (figure 16, h) : coxopodite and basipodite as in earlier stages; terminal joint of endopodite now with eight setae in inner group, six setae in outer group; second joint of exopodite nearly twice as long as first; of joints three to six, the two distal longer than proximal joints; first and second joints together shorter than seventh, seventh over twice as long as four middle joints. No detailed description by Marukawa, but in *E. norvegica* Boeck only twelve terminal setae indicated by Sars on endopodite; gulf of Maine specimens and those described by Nicholls (1934) with thirteen terminal setae as in *E. japonica*.

Mandible (figure 16, l).: second joint of endopodite now bears nine terminal setae. Appendage not described by Marukawa. In *E. norvegica* only eight such setae figured by Sars but Nicholls indicates nine as in *E. japonica*.

First Maxilla (figure 17, c) : gnathobase now bears eight spike-like bristles and five longer plumose bristles; epipodite as in stage V; first lobe of endopodite bears three setae, second, three long and one short setae, third, four terminal setae; exopodite as in stage V. In *E. norvegica* one less seta on exopodite, only

FIGURE 17. *Euchaeta japonica* Marukawa. Copepodid stages x 16.6. IV, first maxilla,—a, second maxilla,—e, maxilliped,—i, first leg,—m; V, first maxilla,—b, second maxilla,—f, maxilliped,—j, first leg,—n; VI ♀, first maxilla,—c, second maxilla,—g, maxilliped,—k, first leg,—o; VI ♂, first maxilla,—d, second maxilla,—h, maxilliped,—l, first leg,—p.

eleven bristles on gnathobase but nine setae on epipodite as observed by the writer. Nicholls describes thirteen setae on endopodite and fourteen on gnathobase.

Second Maxilla (figure 17, k): first and second joints of endopodite each with additional fine smooth bristle. In *E. norvegica* appendage similar.

First Leg (figure 17, o): coxopodite now bears tuft of fine hairs on inner margin; outer margin of first joint of exopodite finely setose at base of distal spine. Setose margin of coxopodite and exopodite not indicated by Marukawa. In *E. norvegica* two spines on outer margin of first joint of exopodite.

Second Leg (figure 18, c): appendage similar to stage V, proximal outer margin of third joint of endopodite finely setose, more sharply indented; long outer spine of terminal joint now extends almost to distal margin of joint. Marukawa does not indicate projection on proximal outer margin of endopodite or seta on inner margin of first joint of exopodite. Joints more elongated in *E. norvegica,* short smooth spines of exopodite not indicated by Nicholls.

The *Third* and *Fourth Legs* as in stage V.

COPEPODID STAGE VI ♂ (figure 16, e)

Length 5.5 to 5.8 mm. Three free thoracic segments, projections on last thoracic segment less pointed than in younger stages; mouth parts considerably reduced, exhibiting retrograde development; second antennae and maxillipeds slightly modified, first maxillae feebly developed, cutting edge of mandible absent, second maxillae completely disappeared. Abdomen five-jointed, first four segments equal, posterior borders finely denticulate, caudal segment short, furca approximately one third length of fourth segment; fifth pair legs large, extending posterior to abdomen and modified as copulatory organs. Mature males observed with spermatophores attached to distal claw of fifth leg, by which fertilizing element is transferred to generative system of female; spermatophores quite commonly seen affixed to vulva. Colouring of male similar to female, ventral surface often golden yellow shading to red. In *E. norvegica,* male noticeably smaller than female, averaging 5.3 to 6.3 mm.

First Antenna (figure 16, e): appendage twenty-three jointed; joints nine and ten coalesced, not ten and eleven as described by Marukawa. *E. norvegica* described as twenty-two jointed by Nicholls.

Second Antenna (figure 16, i): similar to that of female with slight modifications; seta of coxopodite absent, basipodite with only one plumose seta but longer than in female reaching almost to end of first joint of endopodite; setae on inner distal border of first joint of endopodite absent, represented by one very small spine; terminal joint shorter, with groups of seven and six setae compared to eight and six in female, finely setose along proximal outer border; seta of second joint of exopodite absent. Appendage of *E. norvegica* not described nor figured by Sars as different to that of female; gulf of Maine specimens appeared to be modified as in *E. japonica;* Nicholls does not indicate small spine on first joint of endopodite.

Mandible (figure 16, m): masticatory edge of mandible obsolete, short stout

seta of basipodite absent; first joint of endopodite lacks long seta but bears short spine-like process; terminal setae of second joint nine in number as in female, innermost seta finer than others which increase in coarseness toward outer margin. In *E. norvegica* only eight setae indicated by Sars on endopodite; additional fine seta observed on inner margin in gulf of Maine specimens and described by Nicholls. With (1915) described mandible of *E. norvegica* with well-developed but soft-skinned, manducatory part with four short marginal teeth.

First Maxilla (figure 17, d): appendage much degenerated, smaller, changed in shape to that of female; armature of gnathobase completely disappeared, lobe smaller, quite smooth; two small internal lobes absent; epipodite with only five equal setae; endopodite reduced, little indication of segmentation with three large setae on very small terminal joint, group of about six setae on larger basal joint; exopodite with eleven setae, most internal seta very short and spike-like, second seta finer than others. In *E. norvegica*, appendage very similar.

Second Maxilla (figure 17, h): appendage very small, rudimentary, practically no indication of segmentation and division into lobes; setae reduced in number to thirteen, smaller, flexible, no longer spine-like as in female. Only about seven setae indicated in *E. norvegica* by Sars but Nicholls describes about twelve.

Maxilliped (figure 17, l): appendage considerably smaller than in female, claw-like spines of endopodite transformed into flexible plumose setae; coxopodite bears one long slender plumose seta near proximal border, one long, and one shorter plumose seta about middle of joint, one short spine-like seta and a slender plumose seta near distal border; setae of basipodite same in number, middle one of group tapering gradually, lacking thick base; first joint of endopodite with three long, finely toothed setae and two shorter finer setae, second joint with one long and two shorter setae, third with one long and one very short fine setae, fourth with one long seta, terminal joint with two long equal setae, one long slender and one very short fine seta. In *E. norvegica*, only two setae indicated by Sars, three by Nicholls, on coxopodite; gulf of Maine specimens have as many setae, i.e., five, as in *E. japonica*.

First Leg (figure 17, p): appendage similar to that of female, differing chiefly in exopodite which is three-jointed; first joint finely setose on inner margin, unarmed; second joint finely setose, with one seta on inner margin and short distal spine on outer margin of joint; terminal joint finely setose with three setae on inner margin, one terminal seta, one very short terminal spine and one longer terminal spine, outer margin finely setose; spines of outer margin shorter than in female, less slender. No mature males described by Marukawa but in *E. norvegica*, spine present on outer margin of first joint of endopodite.

Second, Third and *Fourth Legs* same as in female.

Fifth Pair Legs, Right Leg (figure 18, j); *Left Leg* (figure 18, k, l): fifth pair legs now exceedingly large, powerful, extending posterior to tip of abdomen; coxopodite of each leg as in stage V; basipodite of left leg unsegmented, longer and narrower than in stage V, that of right leg very large, broadly rectangular;

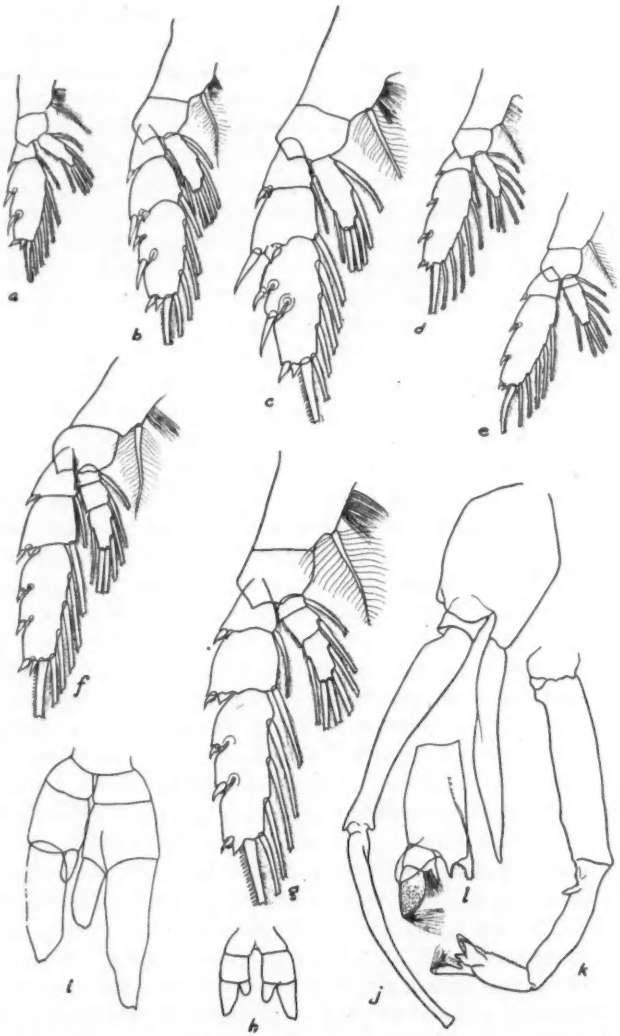

FIGURE 18. *Euchaeta japonica* Marukawa. Copepodid stages x 16.6. IV, second leg,—a, third leg,—d, fourth leg,—e, fifth legs ♂—h; V, second leg,—b, third leg,—f, fifth legs ♂,—i; VI, second leg ♀—c, fourth leg,—g; VI ♂, right fifth leg,—j, left fifth leg,—k, terminal joints of left fifth leg,—l.

endopodite of left leg small, rudimentary, but in right leg, long and styliform, one-jointed, extending to distal margin of first joint of exopodite; exopodite of left leg three-jointed, first joint narrowly rectangular, not as large as basipodite, second and third joints form complicated hand (figure 18, 1); second joint broadly rectangular, terminating in projection or thumb divided distally into two subequal prongs with coarsely dentate margins, row of teeth extends in curving line from external prong along dorsal face of hand; third joint or dactylus not half as long as hand with brush of fine hairs at tip, finely toothed; between third joint and toothed process of second joint arises smooth oval lobe or appendicular lappet and a small pointed setose lobe. Exopodite of right leg two jointed; first joint long and slender as is terminal joint but latter narrower, widening bluntly at tip.

DISCUSSION

Calanus tonsus Brady

This species is closely related to, yet entirely distinct from *Calanus finmarchicus* Gunnerus, the common calanoid of the Atlantic, north Pacific and southern Californian coasts. In the following discussion, the latter species will be used for comparison.

It has already been observed that there are comparatively few distributional records for *Calanus tonsus* and these give no true indication of its relative abundance. In the strait of Georgia, the species dominates the plankton and may represent a case of local concentration. It seems to replace *Calanus finmarchicus* although the latter species is represented there in comparatively small numbers.

The local concentration of this species may be associated with the unusual complex set of conditions found existing in the strait of Georgia. The distribution of an aquatic organism is determined chiefly by the physical and chemical properties of the water in which it lives and variations in the factors of the environment such as are produced by the fresh water of the Fraser river may determine the species and number of organisms that can exist there. Detailed studies of the physico-chemical conditions prevailing in the strait of Georgia have been made by Lucas and Hutchinson (1927), and Lucas (1929). It is probable that the pronounced thermal stratification that exists during the summer months may be a definite limiting factor and the low salinity, increased temperature and distinctly alkaline reaction of the water may appreciably affect the young developing nauplii of some species.

Apparently *Calanus tonsus* not only tolerates the environmental variations which characterize the water of the strait of Georgia but finds in the peculiar set of conditions a particularly favourable environment for its life processes.

Calanus finmarchicus has a much greater range of horizontal as well as vertical distribution than *C. tonsus*. Esterly (1913) found the former species in water 1000 metres deep off the Californian coast, Bigelow (1926) recorded it in the 100 to 170 and 25 to 100 metre strata from the gulf of Maine, while Russell (1925) observed the species to frequent the 30 to 40 metre layer at Plymouth.

The writer has noted *Calanus finmarchicus* as an abundant, though not always dominant, species from the gulf of Maine in the 50 to 100 metre stratum. The distribution depends, naturally, upon the time of the year, the stage of development, and physiological state of the animal.

Calanus finmarchicus is seemingly unaffected by quite definite changes in the temperature and salinity of the water as is *Calanus tonsus*. Bigelow (1915) seldom found *Calanus finmarchicus* in water warmer than 16.9°C. but the temperature varied from 5.3°C. to 24.4°C. Cleve's record (1900) was 7.8°C. A few of the salinity records are as follows: Bigelow (1926), 32.7 to 33.4 (18.09 gm. Cl. to 18.4 gm. Cl. per l.); Cleve (1900), 34.3 (18.9 gm. Cl. per l.), and Farran (1929), 35.3 (19.53 gm. Cl. per l.).

The nauplii of copepods are known to be postively heliotropic and the presence of large numbers of nauplii of *Calanus tonsus* during March and April near the surface is a phenomenon characteristic of the group. The examination of depth hauls of plankton collected every month in the strait of Georgia indicated that as the individuals grow older they retreat to the deeper layers of the sea. The fifth copepodid stage and the adults are seldom found above 100 metres except for a short time during the breeding season when the adults come to the surface.

Similar observations have been made on *Calanus finmarchicus* by other investigators. Paulsen (1906) noted "more *Calani* are present in deeper water than on the surface, individuals are younger as we approach nearer the surface and males only seem to occur in deep water". Damas (1905) says "Verticalement, les stades sont répartis de telle sorte que les individus jeunes prédominent à la surface et les adultes vers la profondeur. Il est probable que les *Calanus* gagnent vers la profondeur en avançant en âge." Willey (1919), quoting Gran, stated that *Calanus* descends in deeper water in winter—as soon as the nauplius larva hatches it ascends toward the light, all copepod nauplii being positively heliotropic. Nicholls (1933) observed the nauplii to be most abundant in the 30 metre to surface hauls—and suggested that the nauplii and young copepodites inhabit this region because of the abundance of food in it.

The developmental stages have already been described in detail and compared with those of *Calanus finmarchicus*. The nauplii of *C. tonsus* are slightly larger as a whole, the appendages are more robust and the armature of the coxopodite of the first and second antennae less conspicuous. The nauplii of both species demonstrate an appreciable increase in size from stage I to stage VI, i.e., from 0.28 mm. to 0.70 mm. The most conspicuous feature of the copepodid stages is the gradual degeneration of the mouth-parts culminating in the adult female in the complete loss of crushing and grinding apparatus with the disappearance of the masticatory edge of the mandible. Even the setae of the second antennae are conspicuously reduced and the armature of spike-like bristles on the gnathobase of the first maxilla no longer persists. The second maxilla is reduced in size but only slightly modified otherwise, and the coarse setae of the coxopodite of the maxilliped are absent. In the male a similar reduction of mouth parts occurs but in addition the endopodite of the maxilliped is conspicuously modified.

In *Calanus finmarchicus* the male exhibits some slight modification of the mouth parts, but in the female their structure is unchanged from that of stage V. Degeneration of the mouth parts is not uncommon in the males of other species of copepods but such a definite transformation is somewhat exceptional for the females.

A fairly definite plan of the life cycle of *Calanus tonsus* has been worked out from an examination of plankton hauls taken throughout the year from the strait of Georgia.

Breeding occurs during the spring months. At that time the eggs and nauplii of the species constitute an important element in the zooplankton. By the end of May, all the nauplius stages and early copepodid stages are passed through.

The species appears to pass the greater part of the year in the fifth copepodid stage. From June 1 to December 11 the plankton samples revealed numerous specimens of the calanoid all at the same stage of development. Apparently the species exists in the adult stage but a short period of the year, January, February and possibly March. The females are believed to die shortly after the reproductive period, as all observed in the strait of Georgia after this period had weak empty bodies and badly broken appendages. Evidence to substantiate this assumption is to be found when the morphological development is studied. The degeneration of the mouth parts and the loss of the chewing apparatus seems to be definitely correlated with the short-lived maturity of the adult.

Here is a case of retrograde development associated with a change in feeding habits. During the summer months when the species exists in the fifth copepodid stage the individuals may feed intensively on the abundant food supply of diatoms available at that time. Specimens of *Calanus tonsus* appear large and fat, filled with oil, and this accumulated food is doubtless sufficient to tide the organism over the egg-producing period. If such be the case, then the reduction of the chewing apparatus is more readily accounted for. Accordingly, the mature females, with the disappearance of all devices for obtaining food, cease feeding and all energies can be expended or diverted to the production of a brood of young.

The males are believed to die shortly after copulation because they are not seen again in the plankton samples after the breeding period. The young individuals of the new generation appear the following winter and attain their short-lived maturity. As for the females, the very feeble development of the mandibles points to the conclusion that the life of the creature is a very short one, death probably following speedily the act of copulation.

Brady's original record for *Calanus tonsus* was presumably for mature females only and these occurred in the plankton February 29, March 29, June 22, October 22 and December 22. Johnson (1932) observed *Calanus tonsus* spawning in the early spring in great numbers at the surface of Puget sound. His record of the species only at this time, together with the continued observations on the species in the strait of Georgia, all furnish evidence of a one year cycle and a definite annual spawning period.

When the life histories of *Calanus tonsus* and *Calanus finmarchicus* are com-

pared they are found to be similar in some respects. Bigelow (1926) and Farran (1927) reported rapid reproduction of *Calanus finmarchicus* during May. Bigelow stated that the species bred little, if at all, in the gulf of Maine from September to October until the following April. Damas (1905) noted that the development commenced in the spring and attained a maximum in the summer. He observed that most of the time was spent in the post-larval stage after which the species lived for a short time as an adult to perish shortly after breeding. At this time the eggs constituted the chief element in the plankton. Nicholls (1933) observed *Calanus finmarchicus* to pass the autumn and early winter in its stage V copepodite form. Lebour (1916) recorded nauplii at the end of January and also in May.

Willey (1919) noted the larval stages II-V on June 2 and July 28. Nordgaard (1905) noted *C. finmarchicus* with attached spermatophores February 7 and February 17. Gran (1902) noted that on May 4, 50 per cent. of *C. finmarchicus* was stage IV, 32 per cent. stage III and 10 per cent. stage V. Herdman (Herdman, Thompson and Scott 1898) noted nauplii at the end of January, in May and at the beginning of July. Thompson (1897) observed that *C. finmarchicus* was not abundant except in the December samples.

Paulsen (1906) stated that the quantities of adult females and nauplii present in the plankton indicated that *Calanus finmarchicus* was in full progress of reproduction in April on the Atlantic coast, south from Iceland, both at the coast and out to sea. Damas (1905) noted males excessively rare, only occurring at a definite season, that of reproduction, or at least fertility, when they abound in certain gatherings in the proportion of one male to three females.

It has been observed that *Calanus tonsus* exists in the adult stage only over a short period of the year. Gran (1902) made similar observations on *C. finmarchicus*—

> "Im Winter wird *Calanus* hauptsächlich nur in der Tiefe gefunden. Wenn die Stromüngen nicht berücksichtigt zu werden brauchten, könnte man also annehmen, das *Calanus finmarchicus* eine einjährige Entwicklung durchgehe, die an der norwegischen Küste im Mai mit dem Tode der erwachsenen Exemplare abgeschlossen werde, während gleichzeitig die neue Generation ihre Entwicklung anfangen müsste. Wenn diese Erklärung richtig sein sollte müssten die zahlreichen jüngeren *Calanus* die im Herbst noch in dem Oberflächenschichten schwimmen, mit dem Eintreten des Winters die Tiefe suchen um dort langsam ihre Entwicklung zu vollenden."

Records have been chiefly concerned with the biology of the species in north Atlantic waters. There it is larger, breeds in the spring and has a one year life cycle. However, *Calanus finmarchicus* is a very cosmopolitan species, its life history varying with its environment. Russell (1925) at Plymouth mentions at least two broods of young per year and Nicholls (1933) observed that reproduction began in February in the Clyde sea-area with three marked breeding periods between February and July. Mr. John Colman, scientist on the Great Barrier Reef Expedition, has informed me of an almost lunar periodicity in the breeding of the species off the coast of Queensland in Australia.

The writer has examined specimens of *Calanus finmarchicus* from the gulf of Maine, and the characters of the adult females lead one to the assumption of the

capability and possibility of two broods. In direct contrast to the situation in *Calanus tonsus*, the females after a reproductive period earlier in the year are healthy in appearance, firm, well filled with stored oil and food materials and there is no sign of degeneration in any of the appendages.

The males of *C. finmarchicus* exhibit some slight modification of the maxillipeds and second antennae but retain the masticatory devices of the mandible and maxilla.

It is possible that if the life history of *Calanus tonsus* were studied in another area, such modifications and variations as are demonstrated in *Calanus finmarchicus* would be found to exist, but in the strait of Georgia the life cycle obviously extends over one year and breeding occurs in the spring followed by the death of the adults.

Euchaeta japonica Marukawa

Euchaeta japonica is one of the largest species of the entire copepod group. One member, *Euchaeta barbata* Brady, reaches the truly gigantic size, for a free copepod, of ten millimetres or more in length of body with the furca and its setae adding another ten millimetres. *Euchaeta japonica* is closely related to *Euchaeta norvegica* Boeck and in this discussion references will be made to the somewhat scanty literature concerning the latter form.

E. japonica as such has only been recorded from the Japan sea and the strait of Georgia. However, there is a possibility that the species *E. elongata* described by Esterly (1913) from the San Diego region was the same. Specimens of *E. japonica* have been observed by this author in plankton samples collected at the Hopkins Marine Station, Monterey bay, California. The writer has noted *E. japonica* as a species of rare occurrence in Puget sound.

Euchaeta japonica is not a common form in the strait of Georgia but is always conspicuous in the deep water hauls due to its large size and conspicuous colouring of red, white and blue. Marukawa (1921) has suggested that it appears to be of the type of northern temperate fauna, found at the surface in the autumn and winter and in the deeper layers during the summer months.

The distributional records for *E. norvegica* indicate that it is also a deep water form. Wolfenden (1904) reported *E. norvegica* in the deep hauls, 500 to 1000 fathoms in the Faröe channel. Bigelow (1926) found it to occur in most horizontal hauls deeper than 100 metres, and Wilson (1932) noted a few females in the bottom net on the 100 fathom line in the outside Atlantic ocean. Bigelow stated that the majority of captures occurred in comparatively high salinity, 33.34 (18.4 gm. Cl. per l.) and from temperatures lower than 10°C. the quantitative occurrence of the species pointing to the higher salinity and to a temperature lower than 8°C. as its optimum.

An examination of depth hauls collected at station I in the strait of Georgia at various times of the year indicates an unusual distribution of the developmental stages. No detailed quantitative analysis was possible due to the nature of the hauls but it appears that *Euchaeta japonica* breeds in the deeper layers and it is

here that the young copepodid stages develop and are found in abundance. Plankton sampies collected January 28, March 24, May 28, June 20 and July 15 all contained nauplii and young copepodid stages in the 400 to 200 metre layer—a decrease in the depth of the haul was accompanied by a decrease in the numbers of younger stages and no nauplii occurred near the surface, i.e., rarely above 100 metres. In the collection of July 15, the nauplii in all stages of development were particularly numerous and far outnumbered the first and second copepodid stages while the older stages were very rare.

This situation is exactly opposite to that found to exist for *Calanus tonsus* and *Calanus finmarchicus* in which the younger stages of development are found near the surface. However, the results obtained for *E. japonica* in the strait of Georgia do not agree with those reported for *E. norvegica* by the majority of the investigators concerned with the latter species. Gran (1902), Wolfenden (1904) and With (1915) all found the younger copepodid stages of *E. norvegica* near the surface. Their findings agree with those already discussed for the two species of *Calanus.*

Störmer (1929), however, records results for *E. norvegica* that do not agree with those of previous investigators but are in concordance with those outlined for *E. japonica* in the strait of Georgia. He suggests that the number of specimens examined was rather small to determine the distribution with any degree of certainty. However, in practically all the plankton samples examined it was noticeable that the smaller copepodid stages are found in deeper water than the larger stages. He did not consider the distribution of the naupliar stages.

During the summer of 1932 the author had the opportunity to examine depth samples from the gulf of Maine which contained specimens of *E. norvegica.* The results obtained strongly substantiate any evidence supplied by Störmer, and it was demonstrated that the youngest copepodid stages only occurred in small numbers at any time but always in the deepest hauls taken and were never found in the upper layers.

The developmental stages have already been described in detail and compared with those of *Euchaeta norvegica.*

The nauplii of *E. japonica* and *Calanus tonsus* differ noticeably in several respects. A conspicuous feature of the naupliar development of *E. japonica* is the very small increase in size from the time the egg is hatched until the sixth stage is reached. The body changes shape very slightly and varies in length from 0.59 to 0.9 millimetres. The body remains practically straight and there is little or no ventral curvature such as is characteristic of *Calanus tonsus.*

In *E. japonica* there is considerable retardation in the development of the naupliar appendages. For example, there is but slight indication of the fourth pair of appendages or first maxillae until the fifth stage is reached, but in *Calanus* they are well developed conspicuous appendages at this stage and are present as noticeable structures in the fourth naupliar stage. In addition, the appendages when compared with the actual size of the body are considerably smaller in *E. japonica* than in *C tonsus.*

This restrained naupliar development is discussed by Nicholls (1934) for *E. norvegica*. He observed the very small amount of growth from nauplius I to nauplius VI and suggested that the species probably does not feed during the larval period, but depends upon the large amount of yolk, some of which is still present even in the sixth nauplius stage.

The copepodid stages of *E. japonica* superficially appear very similar to those of *E. norvegica* but one noticeable point of difference is constant throughout all six stages and proves an easy means of differentiating the two species. The presence of two spines on the outer margin of the first joint of the exopodite of the first leg as compared with one spine in *E. japonica* constitutes this distinctive difference.

The adult females of *E. japonica* do not exhibit the degeneration of mouth parts described for *Calanus tonsus*, but such a retrogressive development occurs in the males of the species and is also characteristic of *E. norvegica*. The very feeble development of the first maxillae, the loss of the masticatory edge of the mandible and the almost complete disappearance of the second maxillae are even more conspicuous than in *Calanus tonsus*. Brady (1883) suggests for the genus that "here we have a case of retrograde development, differing only in degree from the well-known and more conspicuous examples found amongst the lower parasitic Copepoda and the Cirripedes".

Euchaeta japonica does not appear to have such a definite spawning period as *Calanus tonsus* but reproduces more or less all year round, as all stages both naupliar and copepodid are found in the plankton at all times. Females bearing the conspicuous blue egg sacs and males with spermatophores attached to the left fifth feet characterize the plankton throughout the year. It is believed that the females are capable of producing several broods in the one year. Specimens have been observed in which blue eggs showed conspicuously in the ovary while shreds of the old egg sac from which the young nauplii had escaped still remained attached to the genital segment. The lack of any sign of degeneration in the adult females seems to substantiate the argument. The males, however, which exhibit extreme signs of degeneration are believed to die shortly after copulation or after the transference of sperm—the life of the creature in stage VI is probably a very short one and practically devoted to the reproductive process.

The life history of *E. norvegica* has received little attention but Bigelow (1926) observed that the vertical distribution of the species proves that reproduction takes place entirely below 100 metres though occasional individuals in breeding condition may appear at the surface. He noted that *E. norvegica* occurred in the mature stage all year round. Willey (1919) noted females with ovisacs on July 23, August 9 and September 5 and recorded the second copepodid stage on June 26. With (1915) observed adult females with egg sacs or spermatophores and also males. The adults occurred in the 500 to 600 fathom stratum, a few young specimens were found between 100 metres and the surface, and undeveloped individuals were not uncommon near the surface.

SUMMARY

Calanus tonsus Brady

1. It is the most abundant copepod in the water of the strait of Georgia, dominates the plankton and constitutes an important element in the food of fishes.

2. Its occurrence in such abundance in this restricted area may perhaps be attributed to the peculiar set of conditions which exist there as a result of the mixing of the fresh water of the Fraser river with the salt water of the strait.

3. It is closely related to, yet entirely distinct from *C. finmarchicus* Gunnerus, the common calanoid of the north Atlantic.

4. It occurs in greatest abundance in the 200 to 100 metre stratum but is often found in large numbers below that depth and in fewer numbers above it.

5. It appears to complete its development in one year in the strait of Georgia.

6. It has a fairly definite spawning period and at this time the mature individuals come to the surface. Breeding occurs in the spring during March, April and May.

7. The fertilized eggs are deposited singly in the water where they float freely and accumulate in the upper layers.

8. During its development from the egg to the adult, it is characterized by a distinct metamorphosis and passes through a series of six nauplius and six copepodid stages.

9. The eggs, nauplii and younger copepodid stages are conspicuous in the peripheral regions of the strait during the early spring months.

10. The greater part of the year—May to December—is spent in the post-larval or fifth copepodid stage. At this time, it forms an important source of food for such fish as herring and pilchard.

11. During the period when it is found in stage V, an abundant food supply is available. In the strait of Georgia, June, July and August are months of maximum abundance for diatoms, which constitute the chief source of food for the small crustaceans.

12. It exists as an adult for but a short period of the year—approximately two months, January and February. The attainment of maturity is accompanied by a marked degeneration of the mouth parts in both males and females and death follows shortly.

13. The life histories of *C. tonsus* and *C. finmarchicus* are similar as to definite time of breeding and prolonged duration of the fifth copepodid stage.

14. The most conspicuous feature in its development is the reduction of the mouth parts and chewing apparatus in the adult females as well as in the males. In this respect *C. tonsus* differs from the majority of Calanoids.

15. The individuals in stage V feed freely on the abundant food supply available at the time and store up reserve food. In the short-lived sixth stage, the primary function is reproduction and all energies are expended toward this end.

16. The nauplius stages of *C. tonsus* and *C. finmarchicus* are quite similar, but the armature of the appendages is less developed in the former species and the nauplii are slightly larger.

17. *C. finmarchicus* does not exhibit the degeneration of the mouth parts in the adult female as described for *C. tonsus*. The males show the same retrogressive development in both species.

18. The adults of the two species are readily distinguished due to the large size and absence of teeth on the coxopodite of the fifth legs in *C. tonsus*.

Euchaeta japonica Marukawa

1. It is not an abundant species in the strait of Georgia but due to its large size and vivid colouring it is always conspicuous in the plankton. Due to its limited numbers it is less important as food for higher animals.

2. It is closely related to the Atlantic and Polar seas form, *E. norvegica* Boeck.

3. It is a deep water species and occurs in greatest abundance in the strait of Georgia in the 400 to 200 metre stratum.

4. It exhibits no definite breeding period in the strait but evidence indicates that reproduction takes place throughout the year and more than one brood may be produced by one female.

5. It appears to breed in deep water and the eggs are carried by the female in an egg sac until they are hatched.

6. Nauplii and young copepodid stages demonstrate an unusual vertical distribution in that they congregate in the deeper water layers where development proceeds.

7. The life histories of *E. japonica* and *E. norvegica* appear to be very similar and the younger developmental stages show similar vertical distribution.

8. The nauplii differ conspicuously from those of *C. tonsus* in the following respects—larger size and general shape, slight increase in body length from stage I to stage VI and the retardation of the development of the appendages.

9. The noticeable feature of its development is the extreme degeneration of the mouth parts in the mature male. This characteristic of the males is more conspicuous than that observed for the males of *C. tonsus*. The mature males of *E. norvegica* show the same retrograde development of the mouth parts as do those of *E. japonica*.

10. The first five copepodid stages of *E. japonica* and *E. norvegica* appear similar upon superficial examination but a simple means of differentiating the two species as early as stage I has been determined. The presence of two spines on the outer margin of the first joint of the exopodite of the first leg as compared with only one spine in *E. japonica* constitutes this difference.

11. The mature females of *E. japonica* and *E. norvegica* differ in size and in the nature of the lateral projections of the thorax. The mature males of the two species differ conspicuously in the nature of the terminal joint of the left fifth leg.

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Physical and Biological Conditions in Heavily Fertilized Water

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ABSTRACT

The physical and biological conditions in an experimental pond with concrete walls containing 33 cubic metres of water, initially fertilized with approximately 450 kg. (1000 lb.) of cow manure, were studied intermittently during four years. There was a large production of plankton, but it was subject to marked and sudden fluctuations, and the number of species found was not large. The fertilization caused extreme variations in the light conditions, oxygen content and pH value of the water.

A shortage of nutrient salts is one of the primary limiting factors of plant growth in aquatic habitats. By the addition of fertilizer to the water these salts are supplied directly or indirectly. At the same time, however, other alterations in the condition of the water may be entailed and in turn may be found limiting in their action upon the plankton. Thus, in fertilizing, the ideal is that the good effects should more than counterbalance the bad effects and that the ultimate production of plankton should be at a higher level. No attempt was made to attain this ideal; rather the primary intention of the experiment was to elucidate some of the factors governing the growth of planktonts in relatively stagnant water. This entailed a study of both the physical and biological factors, as well as their interrelations. A very heavy fertilizing is not economical, and may even be considered to create a polluted condition, but it does give extreme and varied results. Physical factors fluctuate within wide limits and planktonts come and go, often in immense numbers as the state of the water becomes favourable or unfavourable. These marked variations in the physical and biological conditions provide a good opportunity for making observations upon the interaction of factors, observations which would not be made if the pH value of the water, for instance, or the number of planktonts, did not fluctuate so widely. As a result we are able to plan more restricted and controlled experiments.

Raveret-Wattel (1887) and Mason (1887) report the apparent success of propagating Entomostraca for fish food by the process of fertilization at a piscicultural establishment at Gremaz, in eastern France, and the former author in a later communication (Raveret-Wattel 1898) describes a procedure practiced

near Rouen, France, whereby a greater production of *Daphnia* and other Entomostraca was accomplished by fertilizing small casks with stable manure. In Germany the process has been quite extensively applied for increasing the yield of carp and tench in ponds. Both organic fertilizers of many sorts and inorganic salts (potassium, calcium, phosphate, nitrate, etc.) have been used with varying success. Many of the reports (reviewed by Davis and Wiebe 1930) give the results in production of fish flesh without much discussion of the physical and biological factors involved, and so need not concern us at this time. Hofer (1916), however, reporting upon a series of experiments carried out in earthen ponds at Wielenbach, Bavaria, shows that the yield of plankton was appreciably raised by the use of organic and inorganic fertilizers. Extensive investigations of the effect of fertilizing with mineral salts upon the productivity in earthen ponds have been done at an experimental station near Oranienburg, Saxony. Pauly (1919) found an increase in phyto- and zooplankton (net-plankton) from 110 to 220 per cent depending upon the conditions of the ponds and the degree and kind of fertilization. Von Alten (1919) reports that the salts gave an important increase in the number of species of algae, particularly Diatomaceae, in the number of individuals, and in the size of many species. Wundsch (1919) says that the bottom fauna was also increased by this procedure, but that the effect was greater in the second year. Jarnefelt (1924, 1926), working in Finland, found that the yield of algae and chironomid larvae was augmented several times by fertilizing water with mineral salts.

In North America relatively few investigations have been made to demonstrate the efficacy of fertilizing water. Embody (1921) secured a large production of mosquito larvae, as well as of certain Entomostraca, by treating water in wooden tubs and concrete and earthen ponds with skim milk. Wiebe *et al.* (1929) and Wiebe (1930) were successful in increasing the plankton production by fertilizing small concrete ponds (530 cubic feet) and larger earthen ponds (approximately 100,000 cubic feet) with both organic and inorganic materials. The production of algae and zooplankton, particularly Crustacea, was decidedly greater.

During 1927 and 1928 the experimental pond used in our investigation was under the observation of Mr. W. S. Hall, to whom the writer is indebted for the data covering that period. In the summer of 1929 no observations were made. The writer has studied the conditions in the pond in 1929 from October 3 to December 9; in 1930 from April 12 to December 8; and in 1931 from April 20 to November 5.

THE POND, THE WATER, AND THE FERTILIZER

The pond is one of a series planned by and constructed under the direction of Dr. A. G. Huntsman at the Atlantic Biological Station, St. Andrews, N.B. It is situated on a hillside, facing westward, and overlooking the St. Croix river. It was so placed that ground water would not enter and the exchange of water be thus limited to precipitation and evaporation unless otherwise

desired. The body of the pond walls was constructed of concrete in proportions of six parts gravel to one part cement by volume. The inner surface was finished with a plaster of one part gravel to one part cement by volume and finally with a wash of cement and water. The construction was completed on May 27, 1927. The pond is round in shape with a diameter of 6.1 metres and the walls slope to a maximum depth of 1.83 metres at the centre. Its volume is approximately 33 cubic metres when filled to within 15 centimetres of the top.

The water supply was the tap water of the Station, coming through iron pipes from Chamcook lake, a lake of the oligotrophic type and lying in a granitic region. The reaction of the water in the lake is usually neutral, but as it comes from the pipes, after having run for some time, it is slightly more alkaline with a pH value of 7.2 to 7.6.

The pond was not fertilized until 1928 when approximately 450 kg. (1000 lb.) of well-rotted cow manure was added on July 10.

THE PHYSICAL AND BIOLOGICAL CONDITIONS

The physical conditions of the water in the pond are closely interdependent among themselves, and in turn with the biological conditions. However it is deemed advisable to give an account of the individual physical factors separately, in so far as they have been studied, and to discuss the plankton under the two headings, phytoplankton and zooplankton. This may cause considerable overlapping and repetition of data, but is probably the most concise manner of presenting the facts.

Light

Comparative readings were made of the light penetration into the water of the pond by a modified Secchi's disc. In 1928 a zinc disc, 5.2 centimetres in diameter, and in 1930 and 1931 a white crucible cover, 3.5 centimetres in diameter, were used. The data from the readings are shown graphically in figures 1,5 and 6.

Three agencies which determine the light penetration into the water may be distinguished. In the first case there are the suspended particles of organic and inorganic material which originate from the fertilizer or the decay of plankton; in the second case, the living forms of plankton; and, in the third case, the coloration of the water due to dissolved substances which are derived directly from the fertilizer as it is added, or from the decomposition of this material as well as the dead plants and animals.

The effect of the suspended particles of fertilizer acting almost entirely alone was observed when the manure was added on July 10, 1928. On July 9 the disc reading was 132 centimetres, while on July 12 this had decreased to 13 centimetres. As time went on other agencies came into operation, but, since there were frequent upwellings of gas from the decomposing layer of fertilizer on the bottom, particularly during the warm weather, bringing considerable of the debris into the water above, the effect of these particles, derived entirely

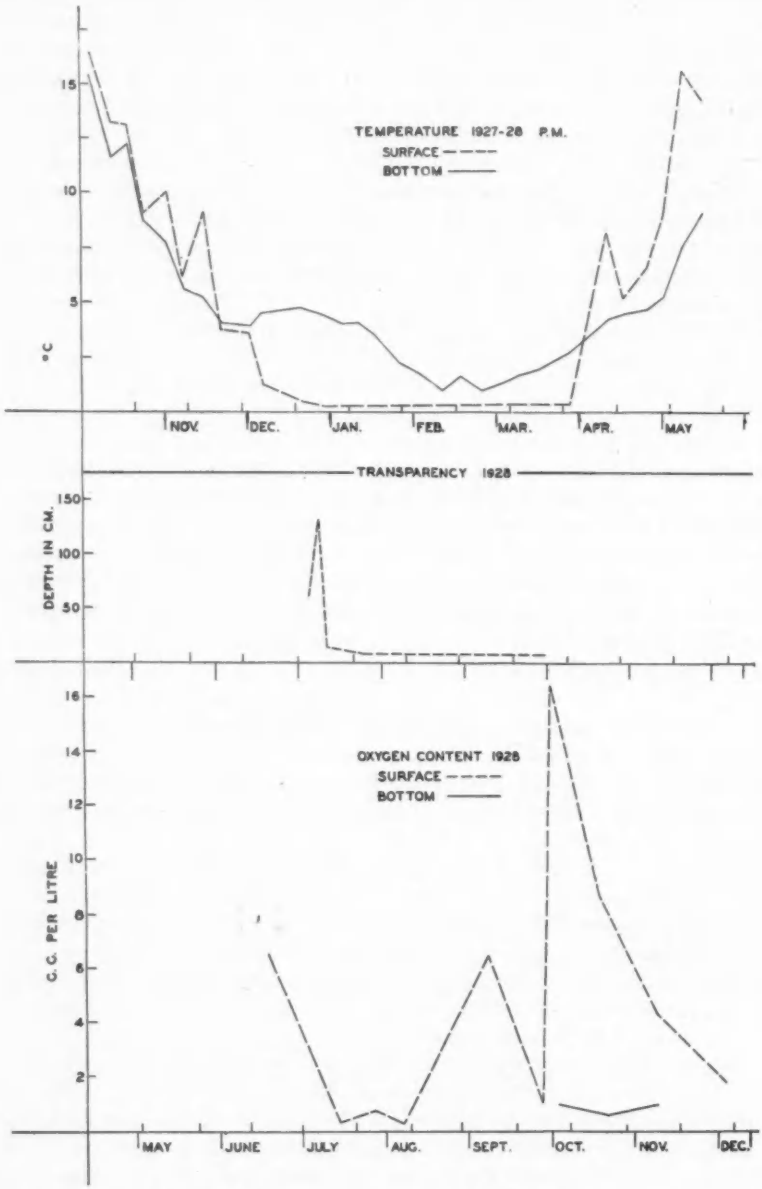

FIGURE 1. Oxygen content and transparency records, 1928. Temperature records 1927-28.

from the fertilizer, continued to be appreciable. However, from year to year the upwelling of gas from the bottom was less frequent, so the effect of these materials declined. In figures 1, 5 and 6 it is shown that, in general, greater depths were recorded for the disc readings in 1930, and again in 1931. It is true that the phytoplanktonic growth may have been somewhat less intense in those years which would also account for a difference.

The action of the suspended particles originating from the decomposition of the plankton began to operate as soon as the first planktonts established themselves. It was rather impossible to ascribe a definite effect to this cause since it was too intimately connected with that of the living plankton. The effect was considered small however because after a heavy growth of plankton had subsided the water of the pond became notably clearer, at a time when it might be expected that those materials would have been most abundant and therefore most effective. Even at such periods the turbidity was not entirely due to this agency, but might have been still influenced, for instance, by the fertilizer or the coloration of the water.

Planktonic, as well as higher plant growths, were important as a factor affecting the amount of light penetrating the water of the pond. In this connection Wiebe (1930) found a definite correlation between the amount of phytoplankton and the transparency of the water in the fertilized ponds that he studied, and in the present investigation this factor was principally responsible for the fluctuations noted in figures 5 and 6. During the summer of 1928 scums of algae formed on the surface of the water with the result that the disc could not be seen below the surface. Rains would drive these forms into the water and the disc would then disappear at 7 or 8 centimetres. By comparing figures 6 and 8 it is seen that in 1931 the pond became clearer as the growth of algae and Ciliata decreased during May. Later in the same year the pond was gradually covered with the duck-weed, *Lemna minor* Linnaeus, so that the light reaching the water of the pond was greatly reduced. That period is represented in figure 6 by the finely dotted line. During September and October the disc readings again decreased as a growth of the colonial alga, *Botryococcus braunii* Kützing, came on. Other algae were scarce in the pond at this time (figures 6 and 8).

The water was definitely stained a brownish-red colour. Its effect upon the transmission of light was difficult to determine as other factors were usually more dominant. Immediately after *Lemna* was cleared from the pond on August 19, 1931, the opaqueness was principally due to this coloration, for at this time the water was comparatively free from suspended organic material.

In this connection Birge and Juday (1930) state that the transmission of solar radiation in fairly comparable, stained, lake waters is materially reduced, and the data of Pietenpol (1918) show that in such waters the short wave lengths of the visible spectrum are absorbed as much, or even more, than the higher red waves, in contrast to that in distilled water, where the absorption of the low wave lengths is least. The colouring matter does not affect so appreciably the transmission of the red or yellow.

As the water of the pond was often quite turbid, the light intensity in the bottom water must have been considerably reduced, and, as light is necessary for photosynthesis, the lack of it at those levels likely became limiting upon the plant growth from time to time. The conditions during the summer of 1928 when the disc was never seen below 7 or 8 centimetres may be cited. Again in 1931 the covering of *Lemna* over the surface of the pond proved a very effective light screen. The phytoplanktonts were practically annihilated and the number of zooplanktonts appreciably lowered (figure 10). No doubt the low intensity of light alone was to a considerable degree responsible for the decreased growth of *Daphnia pulex* (de Geer) and *Heterocypris incongruens* (Ramdohr). In this regard Warren (1900) found that *Daphnia magna* Straus grew and reproduced at a better rate under ground glass and in red light than in green or blue light or in the dark, and Klugh (1927) reports that *Cyprinotus* (*Heterocypris*) *incongruens* grew somewhat less in 50 per cent light and decidedly less in the darkness.

Temperature and Circulation of Water

Records were made of the surface and bottom temperatures of the water in the pond almost daily during the spring, summer and fall. Morning readings were made usually between 9.00 and 10.00 a.m. and those of the afternoon between 4.00 and 5.00 p.m. During the winter of 1927-28 readings were taken approximately weekly by Mr. E. G. Rigby. Air temperatures were also recorded and the general sky and wind conditions noted.

The temperature records for the seasons 1930 and 1931 are plotted in figures 2 and 3. Those for the winter of 1927-28 are presented in figure 1, and are for the afternoon only. The latter temperatures were taken before the pond was fertilized and when the water was quite clear, but they are probably fairly representative for the winter season even after fertilization. The pond froze over on November 21 in 1929 and on December 3 in 1930. On April 12, 1930, the pond was clear of ice.

The surface temperatures of the water were in average a little higher in 1930 than in 1931. The maxima observed for 1929, 1930 and 1931 were 29.5°, 28.6° and 26.8° C. respectively. By comparing figures 2 and 3 it is readily seen that during the early summer the temperature of the bottom water rose more quickly and was at a higher level in 1931 than for the same period in 1930. In 1931 a temperature of 14.8° C. was recorded at the bottom on June 2, while in 1930 a comparable temperature of 14.75° C. was not found until July 10. This condition was due to insufficient mixing of the water, which in turn was caused by a greater phytoplanktonic growth materially affecting the light penetration. A comparison of figures 5 and 6 shows that in average the oxygen content and the pH values for 1930 were at a high level, and that there was a greater divergence between the surface and bottom values than in 1931. Also the water became clearer in 1931 during late May (figure 6). These data substantiate the conclusions regarding the inefficient mixing of the water and the greater phytoplanktonic growth.

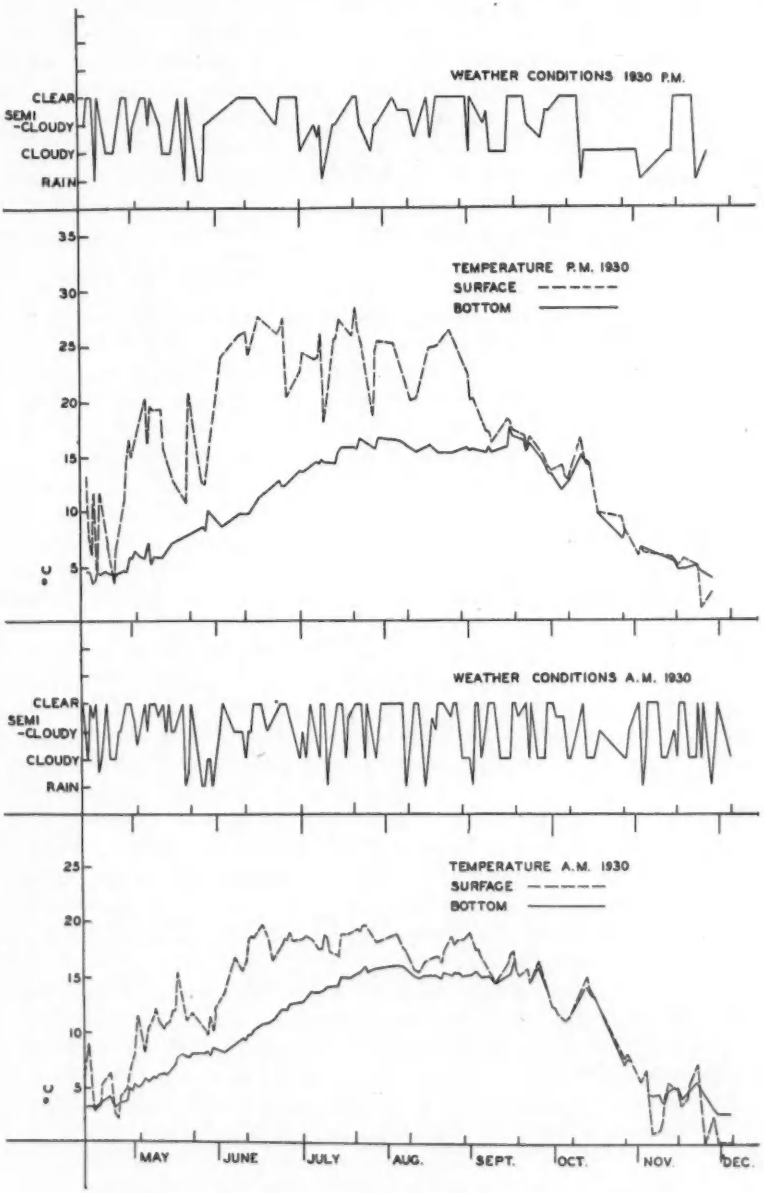

FIGURE 2. Temperature records and weather conditions, 1930.

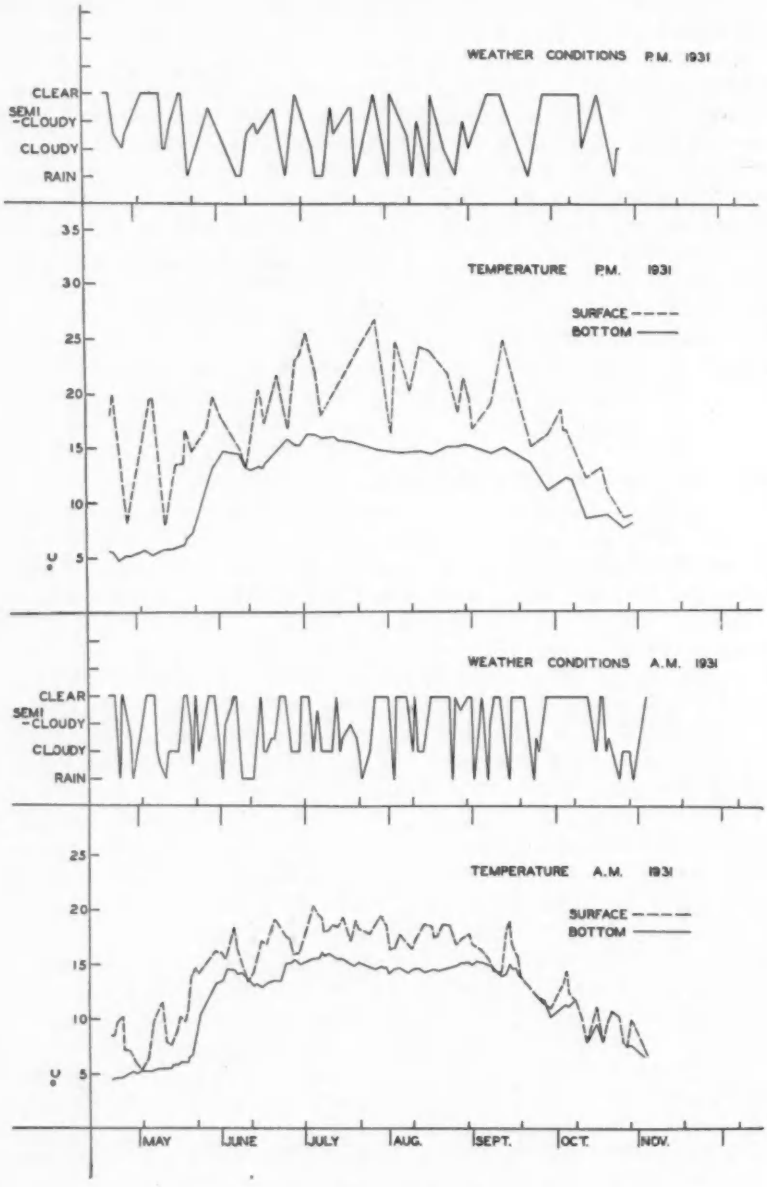

FIGURE 3. Temperature records and weather conditions, 1931.

In figure 4 is plotted the average monthly rise of both the surface and bottom temperatures from morning to afternoon. Included in this figure are the records for pond B1. This pond is situated higher on the hillside, is of the same depth, but was not fertilized so that the water remained perfectly clear. The purpose of presenting these additional data is to illustrate by comparison the effect of the fertilizer upon the temperature relationships.

The rise in the surface temperature of the water was directly correlated with weather conditions, sunshine, wind and air temperature. In 1930 the rise was noticeably greater during June and August than for the same months in 1931, and this corresponds with the records (noted when the temperature of the water was taken) which show more rain and cloudy weather in the latter year (figures 2 and 3). This correlation is particularly apparent for the month of June. Thus, during periods of cloudy weather, and in October and November when the heating effect of the sun is much diminished, the air temperature and wind had the principal influence in place of the direct sunshine.

The rise in bottom temperature from morning to afternoon may also be caused by the direct sunlight if it is able to penetrate to the bottom with any appreciable intensity. But since the water in the pond was for the most part quite turbid, the effect of the direct sunlight was small. The low monthly mean increases shown in figure 4, as well as the discrepancies between the trend of the curves for the surface and bottom temperatures, corroborate this view. There is no definite correlation between the transparency records and the rise in bottom temperature as might be expected. The incompleteness of the data is probably responsible. Conduction from the water above and from the walls, which would reflect the temperature of the earth outside, might also have caused small changes. Conduction is a very slow process in water but would operate to a high degree in the small volume of water contained in the pond. Otherwise it is difficult to explain the rise in bottom temperature when the plant growth excluded practically all of the direct sunlight.

A comparison with the data from pond B1 demonstrates the effect of the turbidity arising as a result of the fertilization. In figure 4 it may be seen that the rise in the surface temperature was least in pond B1, but that the rise at the bottom was greatest during the summer when the light intensity was at its peak. The greater rise in bottom temperature in pond B1 is readily explained by the clearness of the water. The reason for the lower rise in the surface temperature in this pond than in the fertilized pond is that the suspended particles and coloration in the latter effected a greater absorption of the heat rays in the upper layers, while in the clear and unfertilized pond B1 this was not confined almost entirely to the surface, but extended throughout the whole body of the water. There was a correlation in the fertilized pond between the decline of the rise in surface temperature from August to September in 1930 and an increasing transparency of the water (figures 4 and 5). Of course there would be more absorption of the heat rays in the upper layers of both ponds than in the lower, as the red wave lengths of the spectrum are rapidly cut down as they penetrate any body of water.

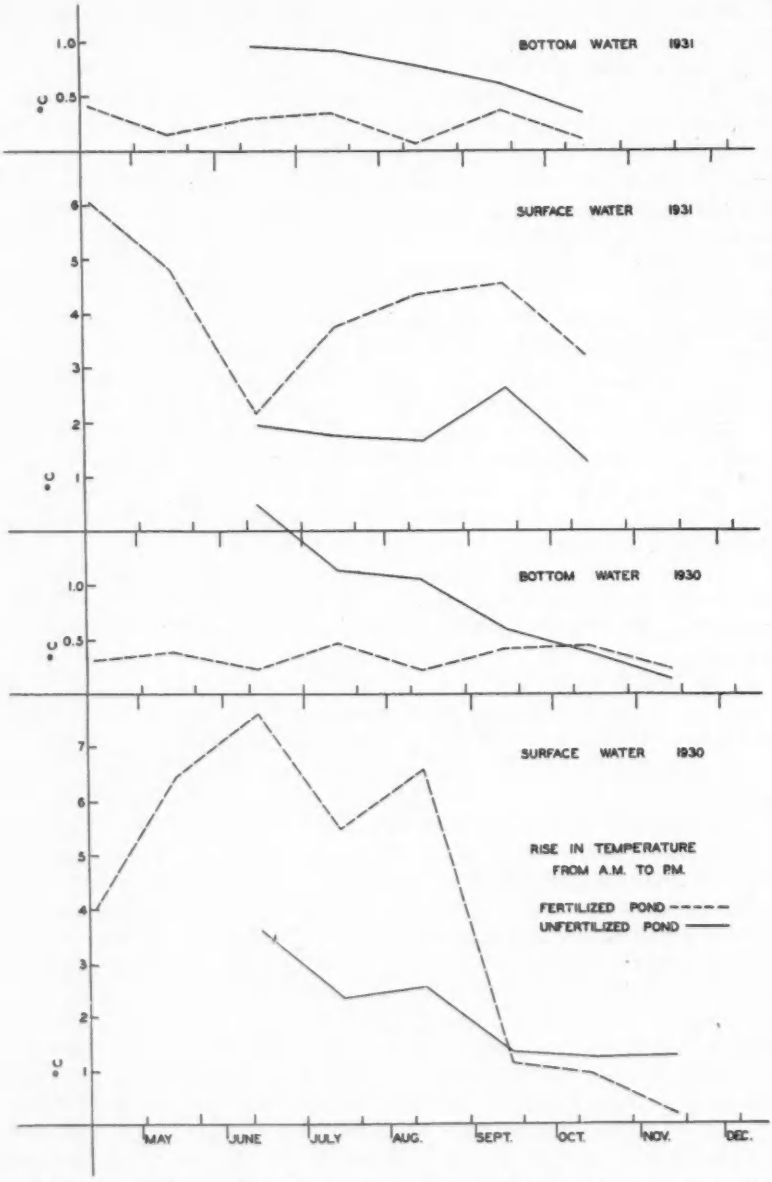

FIGURE 4. Rise in surface and bottom temperature from morning to afternoon, 1930 and 1931.

During the summer season the temperature of the water could hardly be considered as a limiting factor upon the growth, but in the colder weather the low temperature may be effective, and, together with the decreased light intensity, was probably responsible for the decline of plant and animal growth during the winter of 1928-29. In the summer the differences in the temperature of the pond water did not account for the differences in planktonic growth, although Wundsch (1921) found an important correlation between the temperature of the water and the amount of net plankton in fertilized earthen ponds when the production was large. This does not mean that the growth and reproduction of the plant and animal forms were not affected by the variations in temperature during that period, for experiments by McClendon (1910) have shown that *Daphnia pulex* reached maturity in 35 days at a temperature of 4 to 10° C. but only took 6 days at 29 to 31° C., and Klugh (1927) reports that the growth of *Scapholeberis mucronata* (O. F. Müller) and *Cyprinotus* (*Heterocypris*) *incongruens* was also materially increased as the temperature was raised.

TABLE I.—Temperature of the water August 25, 1927 (°C.)

Time	Depth (metres)					
	0.0	0.3	0.6	0.9	1.2	1.5
9.00 a.m.	17.30	17.18	17.00	16.98	16.98	16.98
11.00	17.90	17.65	17.42	17.38	17.35	17.28
1.00 p.m.	20.20	18.55	18.06	18.03	18.00	17.98
3.00	20.70	19.00	18.45	18.39	18.37	18.35
5.00	20.70	19.50	18.73	18.66	18.64	18.62
7.00	19.50	19.42	18.70	18.66	18.66	18.65
9.00	18.90	18.75	18.75	18.67	18.62	18.58
11.00	18.30	18.40	18.45	18.50	18.48	18.35
1.00 a.m.	18.10			18.20		18.20

Early observations indicated that the daily change in temperature might be sufficient to cause an overturn of the water during the summer. These changes are illustrated in the above table for the temperature of the pond water on August 25, 1927. The weather was clear during the day. There was a fair west wind in the morning which changed to the southwest in the afternoon and was of greater velocity. It is seen that at 5.00 p.m. there was a difference of 2.08° C. between the surface and bottom water, but at 11.00 p.m. and 1.00 a.m. the temperature was comparatively equal throughout and lower as a result of the mixing caused by a lowering of the surface temperature to or below that of the bottom. The pond was clear at this time since the fertilizer had not yet been added, and the above data indicate the temperature changes and mixing of the water under such conditions. However once the pond was fertilized and there resulted considerable turbidity in the water, this mixing mechanism did not operate so frequently because the bottom warming from morning to afternoon was not sufficient to bring the bottom water to a temperature which would be equalized at the surface by night cooling. Nevertheless, occasional overturns

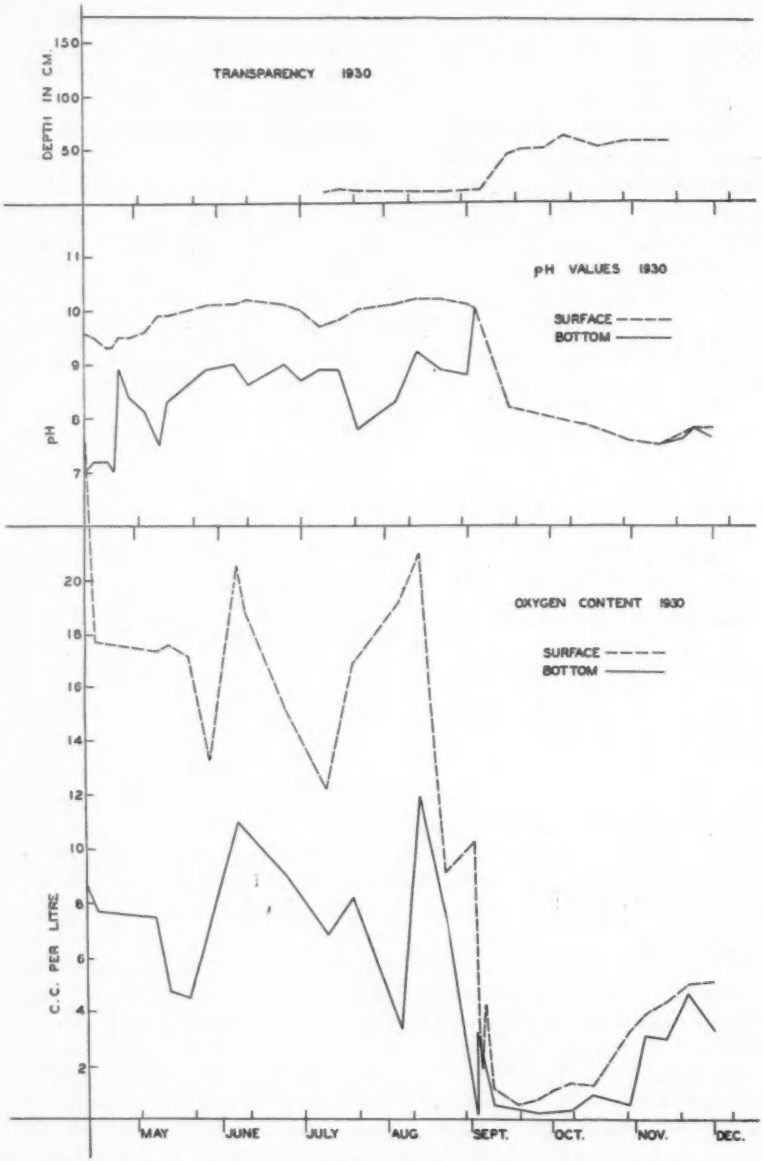

FIGURE 5. Oxygen content, pH values and transparency records, 1930.

evidently occurred in the pond after fertilization as the result of the night cooling. This was indicated by the irregularity in the bottom temperature and the equality of the oxygen content and pH values at the surface and bottom during various intervals in the summer. The temperature records are for not later than 5.00 p.m. and not earlier than 9.00 a.m. so it was impossible to trace the actual temperature changes. These remarks apply principally to the period from May to early September. Before and after that time the air and surface temperatures were lower, regularly low enough nearly every night to equal the bottom temperature, and consequently subsequent mixing was the rule until the temperature of the surface water approached zero.

TABLE II.—Temperature records on certain rainy days (°C.)

Date	Time	Surface	Bottom	Air
1928				
August 8	5.00 p.m.	16.7	16.5	13.8
1931				
June 8	5.00 p.m.	15.0	14.65	13.7
9	9.00 a.m.	14.1	14.1	12.5
9	5.00 p.m.	14.4	14.1	13.4
10	9.00 a.m.	13.3	13.4	11.1
26	5.00 p.m.	16.7	15.8	16.4
27	9.00 a.m.	15.9	15.5	14.5

It was noted that rain and the usual lower air temperature occurring at such times were effective in equalizing the conditions of the water throughout the pond by causing an overturn. Some temperature data are presented above and they illustrate this point. During the summer season these factors were responsible for the most thorough mixing of the water. The overturns are also reflected in the approximation of the oxygen and pH values at the surface and bottom (figures 5 and 6).

OXYGEN CONTENT

The dissolved oxygen content of the water was determined by the Winkler method, except in the late summer and fall of 1928 when the Miller method was employed. The samples were taken in the morning unless otherwise noted, and from both the surface and bottom.

The production of oxygen by the photosynthetic activity of plants is a very well known fact, thus Czensny (1919) and Wiebe (1930) pointed out that the increase of dissolved oxygen was roughly proportional to the amount of algae present in the fertilized ponds with which they were dealing. The former also noted diurnal variations in the oxygen content, depending upon the intensity of the photosynthetic activity, with the maximum amount on clear warm August days at 4.00 to 5.00 p.m. Similar data are recorded below.

In our experiment we consider that the oxygen content of the water was derived principally from the photosynthetic activity of the plants and diffusion from the atmosphere, and that the decay of organic material, the respiration

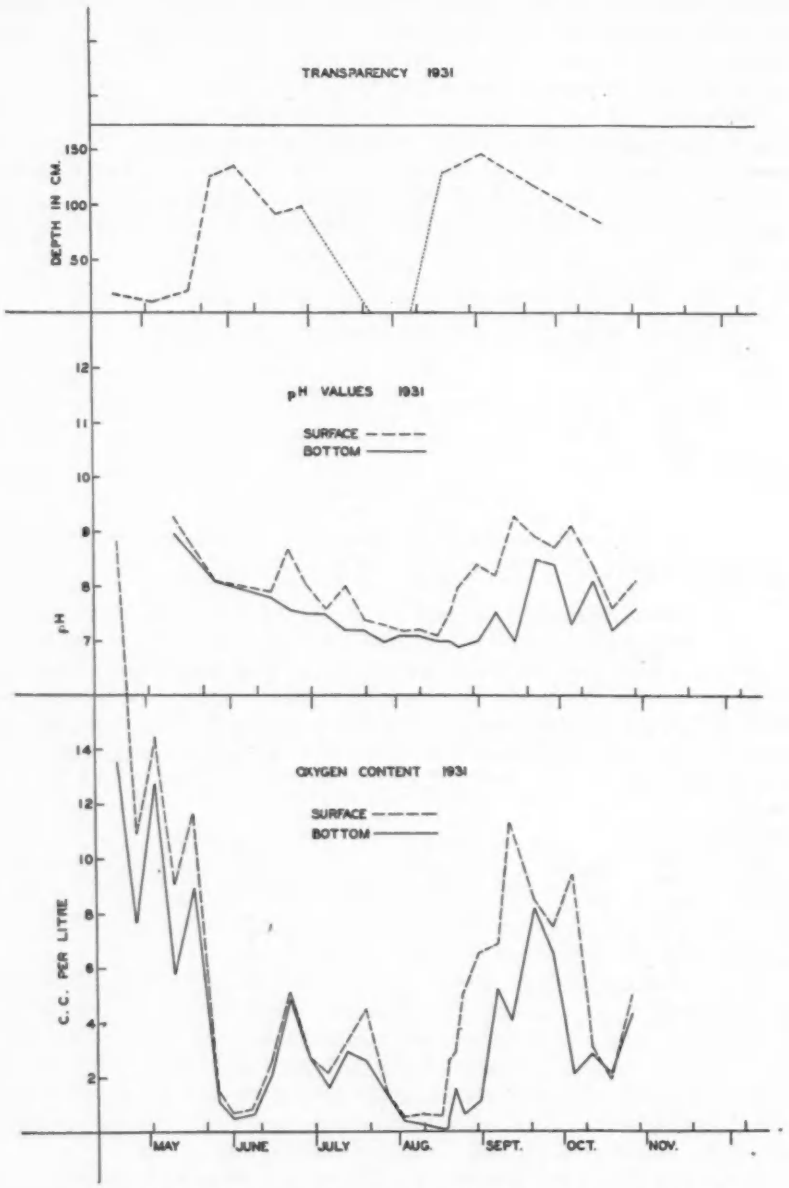

FIGURE 6. Oxygen content, pH values and transparency records, 1931.

of both plants and animals, and diffusion of oxygen to the atmosphere were the factors which tended to deplete its amount. Of these the photosynthetic activity of plants and the decay of organic material were most active in producing the pronounced fluctuations to be noted in figures 1, 5 and 6. The effects of the fertilization were thus manifested very clearly by the action of these two factors. The action produced very high as well as very low values, the fluctuations being quite rapid.

Oxygen was more or less evenly distributed throughout the pond at every overturn of the water. Diffusion of the gas played a minor rôle. Algae were able to carry on photosynthesis at practically all levels except when the turbidity was too great to allow sufficient light to penetrate the water for this purpose. By this production of oxygen in situ even the bottom water received a considerable supply of the gas at certain times (figure 5). The greatest amount of decomposition was, of course, at the bottom where most of the dead organic material was to be found, but the dead organic matter, suspended or sinking in the water, was no doubt responsible for some depletion. The decomposition at the bottom was vigorous enough to almost deplete the oxygen supply at that level if the water did not circulate frequently and there was a paucity of algal growth.

If algal growth was large, the production of oxygen compensated for that lost through decomposition or respiration of plants and animals, and produced a condition of hypersaturation. The surface values were greatest since it was in the surface layers that photosynthesis was most effective, while decomposition was least. During the first half of the season of 1930 the oxygen values at the surface were very high and were maintained within a range from a highest value of 25.05 cc. per litre (10.0° C.) on April 11 to lower values of 9.19 cc. per litre (17.1° C.) on August 21 and 10.31 cc. per litre (20.0° C.) on September 3 (figure 5). The average in the surface water for this period was 16.77 cc. per litre. Even in the bottom water, where decomposition was rife, the plants were sufficient to maintain an average value of 7.66 cc. per litre until August 14. In 1931 the direct effect of the plant growth was again illustrated. By comparing figures 6 and 8 it is seen that the oxygen content fell rapidly as the number of *Chlamydomonas* and other algae decreased during May and June. During late summer and early fall there was a flowering of *Botryococcus* and the oxygen content rose and fell as the growth increased in August and declined in October (figures 6 and 8).

On the other hand, if algal growth was small, the oxygen liberated through photosynthetic activity was not enough to overcome the deficiency caused by decomposition. Thus, in the fall of 1930 the oxygen content of the surface water averaged only 2.33 cc. per litre from September 4 to December 1. The average for the bottom water during the same period was 1.75 cc. per litre. Whereas in the early part of the season the water circulated only at odd intervals, thus effecting considerable discrepancy between the surface and the bottom values, in the fall, to the contrary, frequent mixing occurred, due principally to

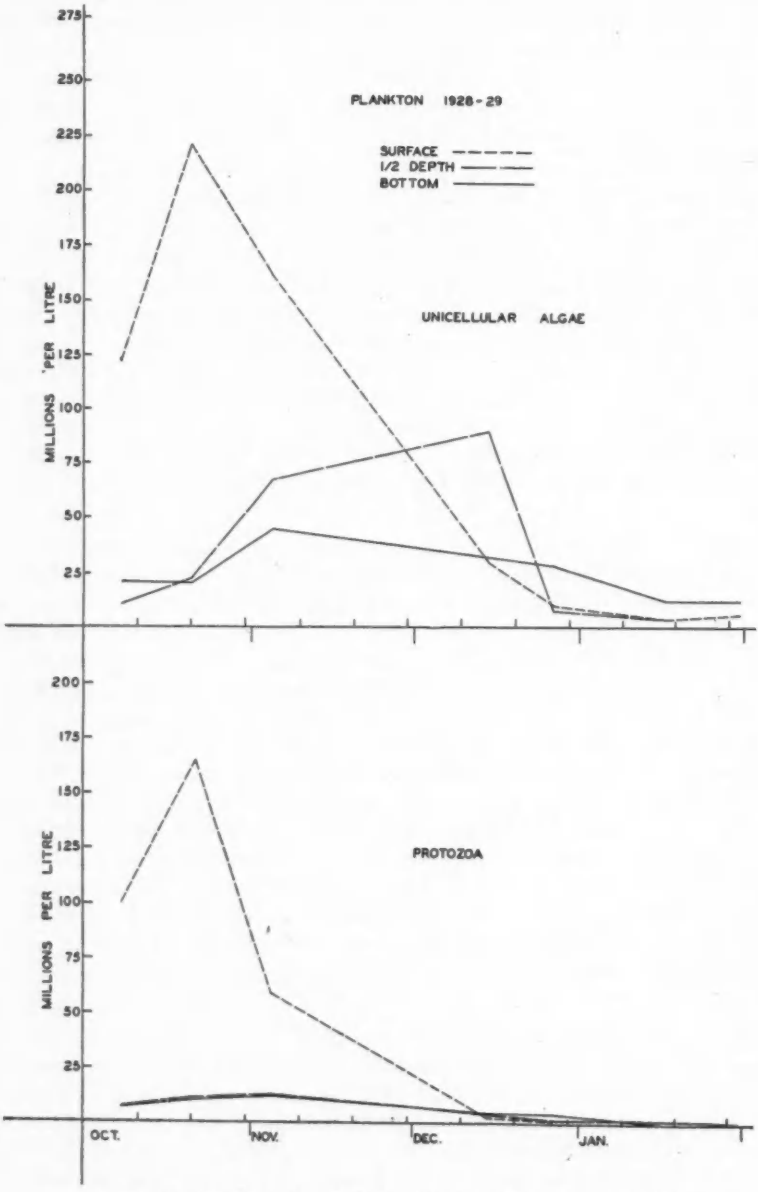

FIGURE 7. Numbers of unicellular Algae and Protozoa, 1928-29.

a greater night cooling of the surface water, with the result that the amount of oxygen in the bottom water approximated that found at the surface.

A transition from a dominance exerted by the photosynthetic activity of the plants upon the oxygen content of the water to one by decomposition was well demonstrated in early September, 1930. As already stated, the algal growth was sufficient until this time to produce a condition of hypersaturation in the surface water. This was also true for the bottom water to about August 14, after which date, however, the value fell, until by September 3 only 0.17 cc. of oxygen per litre (15.5° C.) was present. As the plant growth became scarcer at the lower levels, decomposition became the governing factor of the oxygen content. In the surface water, however, there still remained an abundance of oxygen. On September 3 the weather was cloudy with rain in the morning, and the air temperature dropped below that of the surface water in the pond. The cool weather continued on September 4, and the cooling of the water was sufficient to cause a thorough mixing. The effect was to equalize the oxygen content from surface to bottom (figure 5). The decreasing algal growth was not large enough to overcome the condition of hyposaturation even in the surface water. Subsequent overturns and perhaps the increasing number of *Daphnia* (figure 9) did not permit the diminished quantity of phytoplanktonts to again establish an appreciable oxygen value for any length of time during the remainder of the season (December 1).

The values for the oxygen content plotted in figure 5 are for the morning. Thus on September 4 the oxygen content in the surface water at 9.37 a.m. was 4.01 cc. per litre (17.6° C.), but by 3.37 p.m. the value had risen to 11.46 cc. (20.5° C.). On September 6 the value was 2.56 cc. (16.8° C.) at 8.23 a.m. and 8.65 cc. (20.2° C.) at 2.23 p.m. By September 11, however, the increase from morning to afternoon was appreciably less, 1.14 cc. per litre (14.8° C.) being recorded at 9.00 a.m. and 3.19 cc. (16.1° C.) at 5.00 p.m. It is evident that on September 4 the numbers of algae were adequate to cause a hypersaturation of oxygen in the surface water but were unable to cope with the oxygen-deficient bottom water as it was mixed with that of the surface. Observations and records showed the plant growth was rapidly declining, thus by September 11 the daily increase was much lower.

A fairly steady condition of either hypo- or hypersaturation of oxygen in the immediate surface layer of water indicated the inefficiency of diffusion to equalize the tension of the gas in the water with that in the atmosphere. It is true that the processes effecting either the abundance or paucity of oxygen in the water were always operating, but there certainly was no compensating spontaneous escape or entrance of the gas from or into the water of the pond. The average value of 16.77 cc. of oxygen per litre in the surface water from April 12 to September 3, 1930, gives approximately 250 per cent saturation for the average temperature of the period. The oxygen samples were taken in the morning. During the night the photosynthetic activity of the algae was at a minimum, while the factors tending to deplete the supply continued to operate, but still with that aid diffusion did not lower the surface value below the above

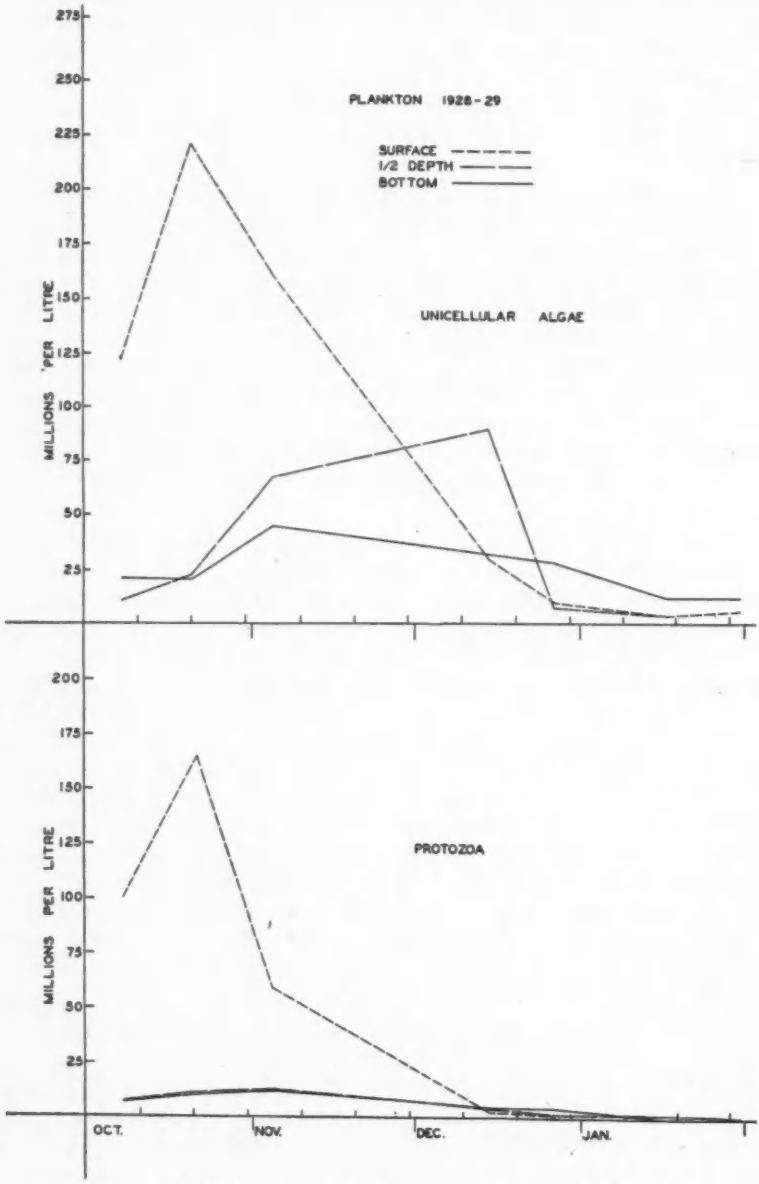

FIGURE 7. Numbers of unicellular Algae and Protozoa, 1928-29.

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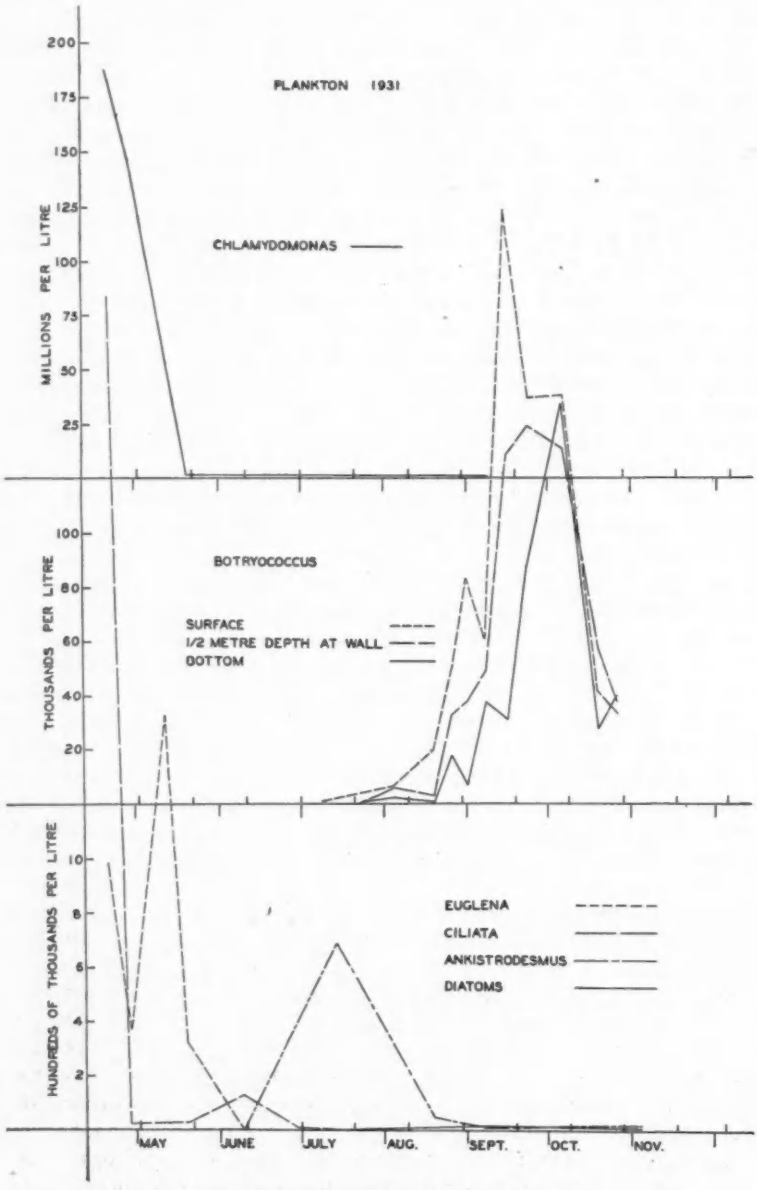

FIGURE 8. Numbers of planktonic Algae, 1931.

average. On August 19, 1931, the mat of *Lemna* which had effectively covered the surface of the pond was removed. In the process the surface water was well agitated. An oxygen content of 0.20 cc. per litre (17.6° C.) was recorded at 9.30 a.m. By 4.30 p.m. the content had risen to only 2.62 cc. per litre (23.5° C.), a saturation value of 44.5 per cent. Considerable agitation of the surface water was necessary before diffusion produced any appreciable effect, and even then with poor efficiency.

Similarly, diffusion of oxygen from layer to layer of water played little part in the equalization of the values. It was not until the water became thoroughly mixed by convection that similar values were found at surface and bottom. Thus, during periods of stagnation marked discrepancies were found although the pond was only 1.83 metres deep.

The data do not indicate that the low oxygen tension which occurred from time to time was necessarily limiting upon the growth of the zooplanktonts, but may have influenced their distribution in the pond. Even when the pond was covered with *Lemna* and the oxygen content was very low throughout the water of the pond numbers of *Daphnia pulex*, *Heterocypris incongruens* and *Cypris pellucida* Sharpe survived although their number decreased. It was impossible to separate the effect of the low oxygen content from the action of other factors which may have been limiting. Red chironomid larvae thrived in the decomposing material at the bottom of the pond where there must have been practically no oxygen. Certain species of chironomids in the larval stages have been found by Juday (1909) and Cole (1921) living in water that contained no oxygen.

Acidity and Alkalinity

Measurements of the acidity and alkalinity expressed as pH values were determined by the colorimetric method for both the surface and bottom water at frequent intervals. Clark's buffer solutions were used in making up the standards, which in turn were checked against the hydrogen electrode method. No attempt was made to ascertain readings to less than 0.1. Any readings above 10.2 were more or less approximate since that was the limit in the range of the indicators employed, but it was concluded from the intensity of the colour that the reaction of the water very rarely went above this value.

The degree of acidity or alkalinity is mainly determined by the relationships between dissolved carbon dioxide, bicarbonate and normal carbonate. An index of the relationship is given by the pH value. Above a pH value of 8.0, the turning point of phenolphthalein, the reaction is such that there exists no free dissolved carbon dioxide in the water. In the pH scale a value of 7.0 indicates neutrality, that is, the amount of hydrogen ions just equals the amount of hydroxyl ions.

The sources of carbon dioxide in the water of the pond were from the decay of organic materials, the respiration of plants and animals, and the atmosphere. Very little was derived from the latter source because of the low tension of the gas in the air. For the most part the source was the decay of organic matter,

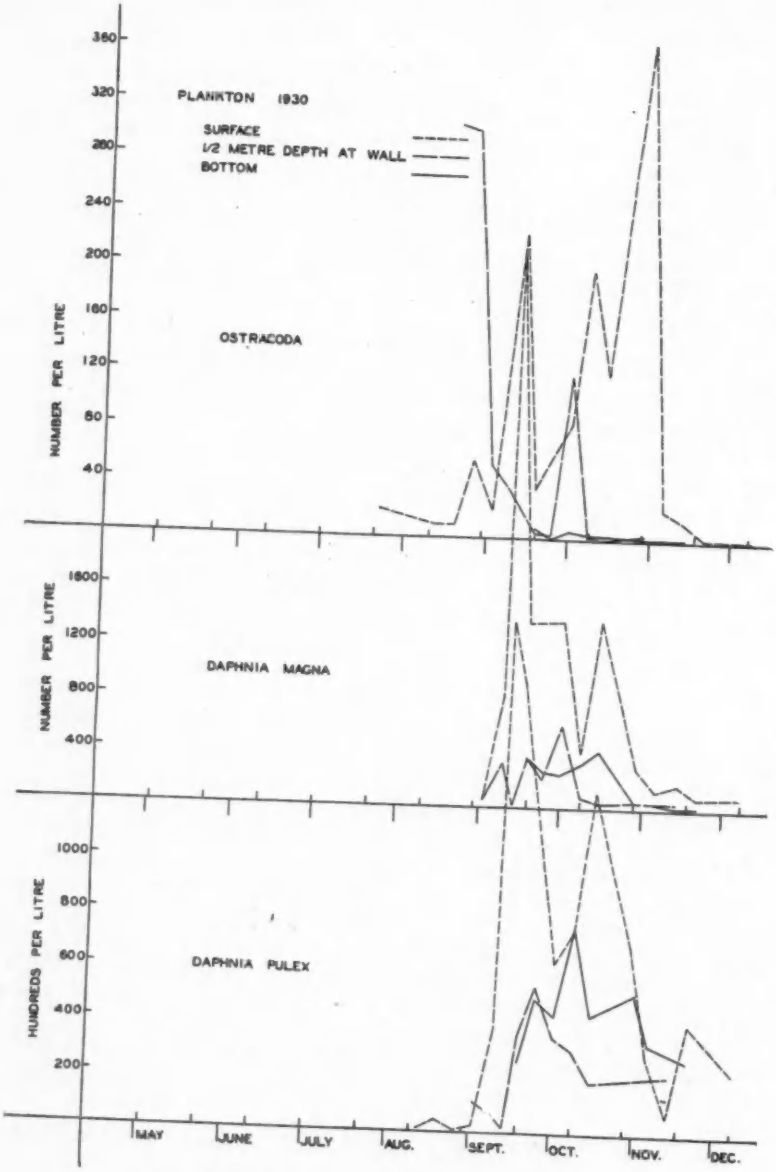

FIGURE 9. Numbers of planktonic Crustacea, 1930.

derived directly from the fertilizer or from the organisms. On the other hand a tendency toward depletion of free carbon dioxide, as well as part of the bicarbonate, was caused by the plants while carrying on photosynthesis.

Since, as with the oxygen content, the decomposition of organic material and the photosynthetic activity of the plants were responsible for the principal fluctuations in the pH values, considerable amplitude in the range of these values was found. For the most part the discussion of the variations in the oxygen content is applicable to the pH values. As may be seen by comparing the figures illustrating the oxygen content and pH values, the trend for each is quite similar, and there exists a definite correlation. There is also a correlation with the planktonic growth (figures 6 and 8). Values as high as 10.2 or slightly above were recorded when the plant growth was large. During 1930 the values ranged from 9.7 to 10.2 from May 10 to September 3. In water with little or no plant growth much lower readings were made. Thus in 1931 the surface records from July 21 to August 22 were 7.1 to 7.5, with those at the bottom being 7.0 to 7.2 (figures 5 and 6).

The concrete of the pond walls had considerable influence upon the reaction of the water. They formed a continual source of calcium carbonate with which the carbon dioxide of the water in contact with them could react, and caused a primary high pH value. When the pond was first filled with water in 1927, the pH value of the water as it entered was 7.6 on June 1, but by June 6 the value had risen to 9.8 and gradually increased to 10.0. However the extremes and fluctuations were the direct result of the plant growth and the decay of organic matter.

In agreement with Hofer (1916) and Wiebe (1930) it is concluded that the plant growth governed the pH values rather than the reverse as far as concerns the species that were found in abundance. Klugh (1927) found that *Cyprinotus* (*Heterocypris*) *incongruens* died at a pH value above 9.0 under experimental conditions, but this species as well as *Daphnia magna*, *D. pulex*, *Scapholeberis mucronata* (O. F. Müller), *Ceriodaphnia quadrangula* (O. F. Müller) and *Cypris pellucida* were taken from the water when the value ranged above 10.0. Although the extremes were not necessarily limiting upon the above species, others, which were introduced and did not reproduce well, as species of copepods, may have been restricted in their growth by such a limiting action. Such may also be applicable to certain plant forms. As was indicated above it was impossible however to definitely ascribe a limiting action to any one factor.

Nutrient Salts

Plants require various inorganic salts for growth and reproduction, among which nitrates, phosphates and silicates are considered important. Hofer (1916) and Wiebe (1930) have found that the content of nitrates and phosphates may be increased in the water by fertilization with organic materials even if the plant production was much greater. Some determinations of the phosphate content were made by Dr. John M. Morton. Due to the coloration of the water the readings were difficult to make and affected the accuracy of the results to some

degree. Dr. E. J. King also made some determinations of the silicate content. In the following table all samples were from the surface unless otherwise indicated.

TABLE III.—Phosphate and silicate of the water, 1931

Date		Milligrams of P_2O_5 per cubic metre	Milligrams of silicate per litre
July	15	10570	34.38
	22		32.27
	27	5100	
August	3	7500	
	18		30.60
			33.60 (bottom)
	19	9180 (bottom)	
September	4	11010 (bottom stirred)	
	5	8175	
		9950 (bottom)	
	14		24.50
			25.60 (bottom)

PHYTOPLANKTON

Quantitative records of the phytoplankton are available only for the fall and winter of 1928-29 and for the summer season of 1931. In 1931, 300 cc. samples from the surface of the pond were centrifuged, the samples then made up to 10 cc. and counts made with a Sedgwick-Rafter counting cell. The number per litre was calculated from these counts.

The phytoplanktonic growth in the summer of 1928 was dominated by *Chlamydomonas* and *Chlorogonium*, which at times were so abundant as to form a scum upon the surface of the water. The oxygen content at the surface was occasionally quite high as a result (figure 1), although a circulation of oxygen-deficient water from the bottom was common on account of the upwellings caused by gas from the decomposing fertilizer. *Scenedesmus* and pamelloid forms were also present in smaller numbers. *Navicula* was found infrequently. The bacterial flora was quite large, especially at the bottom, and was indicative of the rather foul condition of the water. From October 8, 1928, to January 30, 1929, quantitative records were made (figure 7). The bulk of the unicellular algae was composed of species belonging to the genera *Chlamydomonas*, *Ankistrodesmus* and *Chlorogonium*. Their number decreased as the winter progressed. Colonial algae were also plentiful. On October 8 there were found 40 million colonies per litre at the surface, at half-depth 1.7 million, and at the bottom 1 million. By October 22 the number at the surface had diminished to 9 million, but remained more stationary at half-depth and bottom with 1.3 million and 1 million respectively. Later (November 5) there were present 3.3 million per litre at the surface, 2 million at half-depth, and 3.3 million at the bottom. In contrast with October 8 and 22 the distribution on this date was quite uniform throughout the pond. Such may have been caused by an accumulation of the older colonies in the lower water, or by a more thorough mixing of the water.

By December 27 the colonial algae had entirely disappeared. *Navicula* was also enumerated for the surface water and 15 million per litre on October 8, 5 million on October 22, and 1.8 million on December 15 were found. The number had declined to 1,700 per litre by January 30.

Scenedesmus was very abundant during the fall of 1929 and *Ankistrodesmus* and *Chlamydomonas* were also present in fair numbers. A very heavy culture of a short, stout, bacillus was found to constitute a large part of the mass of organisms.

Qualitative samples from the pond for the summer of 1930 showed an abundance of pamelloid forms until late August, when, coincidently with the decline in oxygen content and pH values, the numbers decreased markedly. For the same period *Chlamydomonas*, *Ankistrodesmus* and *Navicula* appeared in minor quantities. Bacteria were present during the entire season, but, judged from the qualitative samples, they were much less abundant than in the previous fall. The oxygen content and pH values were again indicative of the small algal growth in September, October and November.

Chlamydomonas was the dominant form in the spring of 1931. The greatest number, 187,237,500 per litre in the surface water, was recorded on April 21. The form rapidly declined in abundance during May, after which time the numbers remained small so that on September 9 only 1,250 per litre were taken. *Ankistrodesmus* and *Navicula* were recorded in less quantities (figure 8). The diatom occurred in late summer and fall and never went above 7,500 per litre. *Scenedesmus* was only taken once (May 10) when there were 1,875 per litre. In mid-summer the conditions in the pond were dominated by a growth of *Lemna minor* (*Lemna* is not a planktonic form but a spermatophyte which floats on the surface of the water). By July 15 the pond was nearly covered. This was decidedly detrimental to the plankton as seen by the decrease in quantity during July and early August (figures 8 and 10). Also as indicated above the oxygen content fell to low values and the acidity increased (figure 6). The *Lemna* was entirely removed on August 19. The phytoplanktonts which had occurred earlier in the season increased little, if at all, but their place was taken by a "bloom" of *Botryococcus braunii* (figure 8). It reached its peak of abundance in September, when on September 16 there were 216,667 colonies per litre in the surface water. Once again a correlation between the oxygen content, pH values and the algal growth was well shown.

ZOOPLANKTON

The quantitative samples were taken by dipping and straining through a number 18 plankton net 10, or in some cases 9, litres of water. The samples were then made up to 100 cc. and from 20 to 100 per cent of the sample examined and the organisms enumerated.

A feature of the zooplanktonic growth in the pond during the summer of 1928 was the abundance of Ciliata, principally of the genera *Cyclidium*, *Oxytricha* and *Chilodon*. These forms are common in stagnant water and infusions of various sorts and may be considered as indicative of the "polluted" condition

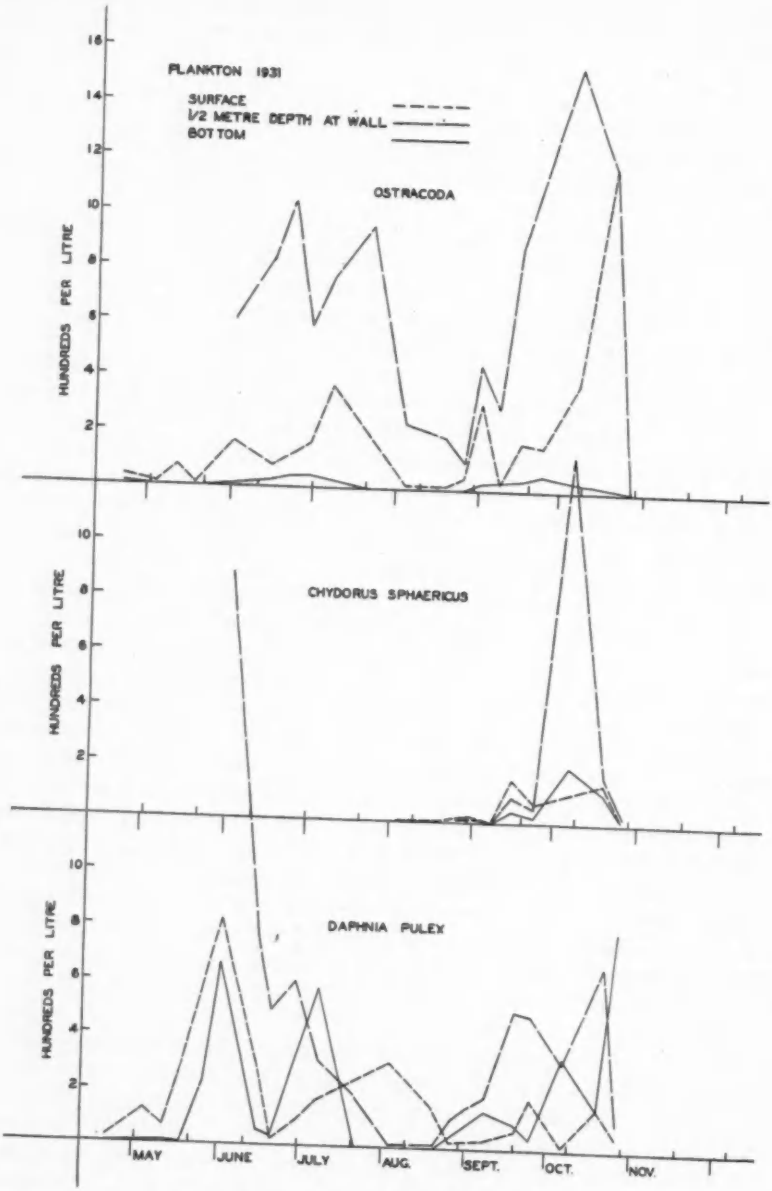

FIGURE 10. Numbers of planktonic Crustacea, 1931.

caused by the cow manure. The presence of the rat-tailed maggot, *Eristalis*, was also additional evidence. Larvae and pupae of mosquitoes and chironomids were abundant. In spite of the seemingly adverse conditions the cladoceran, *Alonella* sp., and the copepod, *Cyclops viridis* (Jurine) were taken in scanty numbers. Quantitative records were made from October 8, 1928, to January 30, 1929, and the number of Ciliata in the samples are plotted graphically in figure 7.

By the fall of 1929 Ciliata were few but their place was occupied by an abundance of Flagellata, *Trachelomonas hispida* Stein, *T. lagenella* Stein, or a very closely related species, and *Euglena viridis* Ehrenburg. *Ceriodaphnia quadrangula* and *Scapholeberis mucronata* were fairly abundant in October, but both had entirely disappeared by November 18. *Eucyclops serrulatus* (Fischer) was quite common and females bearing egg sacs were noted. Copepod nauplii, presumably *E. serrulatus*, were taken in the hauls during October. The ostracods *Heterocypris incongruens* and *Cypris pellucida* were recorded for the first time in the pond. Chironomid larvae (blood-worms) and pupae were still common, and the corixid, *Callicorixa canadensis* Walley was observed in small numbers.

In the spring of 1930 the species of *Trachelomonas* and *Euglena* were still present but their number decreased rapidly, and they had totally disappeared by May 30. The rotifer, *Philodina citrina* Ehrenburg, was taken but had also gone by June 13. *Scapholeberis mucronata* was noted in only sample taken on July 16. On June 9 several specimens of *Daphnia pulex*, and later in August of *D. magna*, were introduced into the pond. *D. pulex* increased in numbers during June, July and August but for some reason the conditions in the pond brought on sexual reproduction, for as early as August 8 ephippial eggs were produced. However in September and October the species flourished in greater numbers and on September 14 there were 1,895 individuals per litre in the surface water (figure 9). During the same period *D. magna* reached its peak of abundance. On September 14, 4,220 specimens per litre were taken in the surface water (figure 9). *Heterocypris incongruens* and *Cypris pellucida* were abundant after May, especially the former (figure 9). It was observed that *Heterocypris incongruens* would collect in more or less compact swarms just under the surface of the water in the shadow of the walk across the pond, or in the open when the sun was semi-bright as when it shone through a haze of cirrus clouds. This phenomenon did not take place on very dull days or when the wind rippled the surface of the water. These observations indicate that there was an intensity of light more conducive to this peculiar habit between the bright sunlight and the complete obscurity of the sun.

Daphnia pulex was again found in large numbers in 1931 with a maximum of 2,301 per litre at the half-metre depth near the wall on June 2 (figure 10), but *D. magna* did not reappear during the entire season. In September and October *Chydorus sphaericus* (O. F. Müller) became numerous; the maximum was 1,338 individuals per litre at the half-metre depth on October 7 (figure 10). *Heterocypris incongruens* and *Cypris pellucida* were also found in abundance, the former constituting approximately 95 per cent. of the culture (figure 10). Aside from these forms some Ciliata and a few *Philodina citrina* were the only zoo-

planktonts taken in the net samples. Mosquito and chironomid larvae and pupae were decidedly less numerous than in the previous years.

For the forms occurring in the pond during 1929, 1930 and 1931, the specific determinations of Cladocera and Copepoda were checked by Dr. C. Juday and Dr. C. D. Marsh; and Rotatoria were determined by Mr. Frank J. Myers, Ostracoda by Mrs. V. Lucas Smith, and Insecta by Mr. G. Stuart Walley.

GENERAL SUMMARY AND CONCLUSIONS

1. The physical and biological factors in a concrete experimental pond, containing 33 cubic metres of water and fertilized with approximately 450 kilograms (1000 pounds) of cow manure, were studied intermittently during four years.

2. The transparency of the water in the pond was decidedly lowered by the coloration of the water and, at times, by the large growth of plankton. Thus, although the daily rise in temperature from morning to afternoon was considerable at the surface during the summer season, the turbidity of the water permitted only a comparatively small increase in temperature at the bottom.

3. A cooling of the surface layer at night caused fairly regular overturns of the water during the early spring and the autumn, but only irregularly in the summer as the warming of the bottom water during the day was not sufficient to bring the temperature of this water above the value to which night cooling reduced the surface water. A cold rain, together with a lower air temperature, was effective during the summer season in overturning the water.

4. The temperature of the water was not a limiting factor for the planktonic growth in the summer, but evidently became so during late autumn and winter.

5. The oxygen content was controlled principally by decomposition of organic material and by the photosynthetic activity of the phytoplankton. Thus the fertilization caused extremely wide variations and rapid fluctuations. A persistent hypo- or hypersaturation of oxygen in the immediate surface layers of the water demonstrated the inefficiency of diffusion to equalize its tension in the water with that in the atmosphere.

6. The alkalinity of the water was notably high. The pH values fluctuated also as a result of decomposition and photosynthesis, and there existed a definite correlation between the oxygen content, pH value, and the phytoplanktonic growth. The concrete walls of the pond were responsible for a basically high alkalinity, but the variations, often extreme, were caused by the factors indicated above. Owing to the high alkalinity, little or no free carbon dioxide would have existed in the water, except during periods of decided stagnation.

7. Neither the low oxygen content nor the high alkalinity of the water could be demonstrated as limiting the growth and reproduction of the majority of plants and animals found in the pond. However these factors may have had a restrictive action upon several forms, as copepods, which were at times present but never became abundant.

8. There was an extremely high content of dissolved phosphates and silicates in the water during 1931.

9. The fertilization was very effective in producing large growths of various planktonic plants and animals, although the number of species which were found was not large. The production was subject to marked and sudden fluctuations, and there was a succession of forms from year to year. Such an experiment in which the fertilization may be considered excessive is of value as being indicative of the extreme conditions that certain plant and animal planktonts are able to withstand.

10. A carpet of *Lemna minor* was quite detrimental, as it decreased the amount of light, causing a decided stagnation of the water, with the result that the oxygen content, pH value, and the planktonic growth were appreciably lowered. *Lemna* and similar forms have the status of weeds.

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